

THE HEAD AND NECK MUSCLES ASSOCIATED WITH FEEDING IN *SPHENODON* (REPTILIA: LEPIDOSAURIA: RHYNCHOCEPHALIA)

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ABSTRACT

Feeding in *Sphenodon*, the tuatara of New Zealand, is of interest for several reasons. First, the modern animal is threatened by extinction, and some populations are in competition for food with Pacific rats. Second, *Sphenodon* demonstrates a feeding apparatus that is unique to living amniotes: an enlarged palatine tooth row, acrodont dentition, enlarged incisor-like teeth on the premaxilla, a posterior extension of the dentary and an elongate articular surface that permits prooral shearing. Third, *Sphenodon* has a skull with two complete lateral temporal bars and is therefore structurally analogous to the configuration hypothesised for the ancestral diapsid reptile. Furthermore, the fossil relatives of *Sphenodon* demonstrate considerable variation in terms of feeding apparatus and skull shape. Lastly, as *Sphenodon* is the only extant rhyngocephalian it represents a potentially useful reference taxon for both muscle reconstruction in extinct reptile taxa and determination of muscle homology in extant taxa.

Here we provide an up-to-date consensus view of osteology and musculature in *Sphenodon* that is relevant to feeding. Discrepancies within previous descriptions are evaluated and synthesised with new observations. This paper displays the complex muscle arrangement using a range of different imaging techniques and a variety of different angles. This includes photographs, illustrations, schematic diagrams, and micro-computed tomography (micro-CT) slice images.

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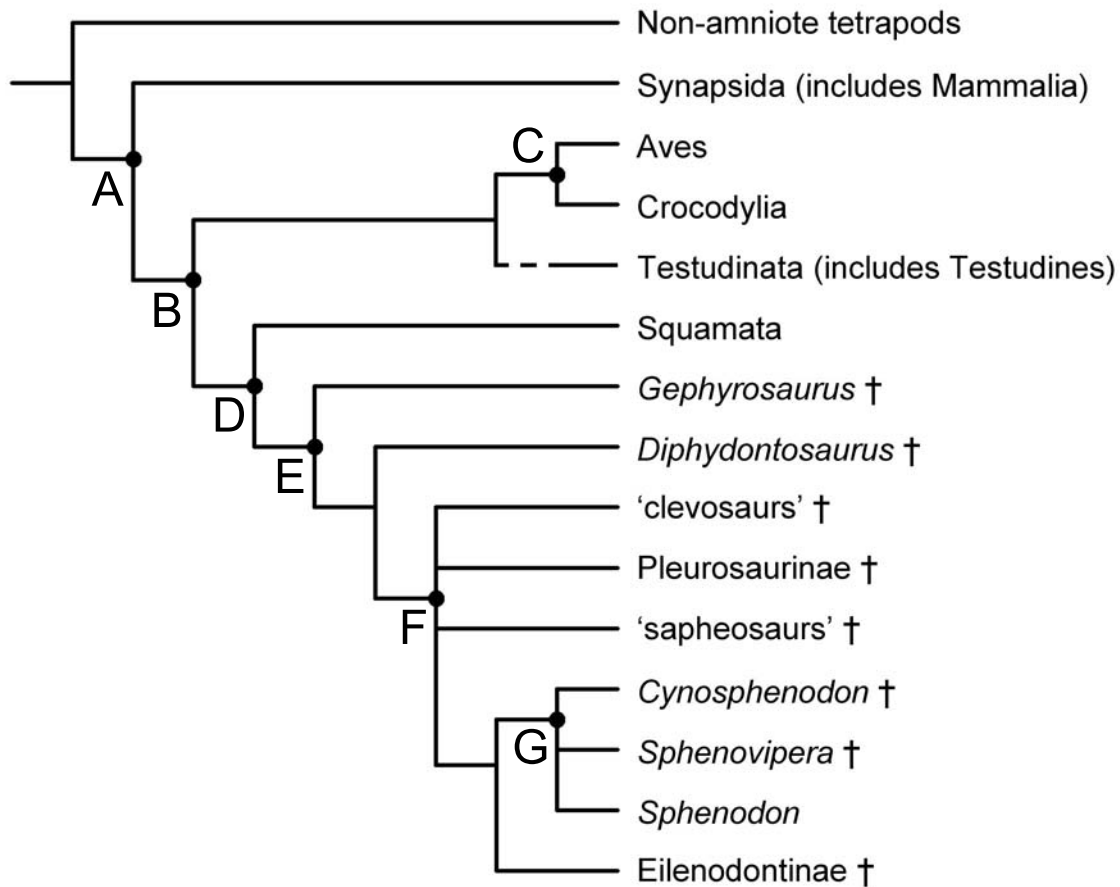


FIGURE 1. Composite cladogram demonstrating the evolutionary relationships of *Sphenodon* and other Rhynchocephalia to other amniotes. Dagger designates extinct clade. Based on data from Evans 1988, 2003; Reynoso 1996, 2000; Zardoya and Meyer, 1998, 2001; Evans et al. 2001; Apesteguía and Novas 2003; Rest et al. 2003. Nodes: A, Amniota; B, Diapsida / Reptilia; C, Archosauria; D, Lepidosauria; E, Rhynchocephalia; F, derived rhynchocephalians; G, Sphenodontinae.

INTRODUCTION

Sphenodon (tuatara) represents the only living member of the Rhynchocephalia (*sensu* Gauthier et al. 1988), a group that was diverse and globally distributed for much of the Mesozoic (Evans et al. 2001; Jones et al. 2009). Because of its uniqueness, *Sphenodon* has an iconic status in New Zealand (e.g., Acres 1990; Daugherty and Cree 1990; Mlot 1997; Stephens and Lambert 1998; Baynton 2001; Parkinson 2002; Darroch 2005; Ramstad et al. 2007), and serious efforts are being made for its conservation on the 35 offshore islands it inhabits (e.g., Schmidt 1953; Daugherty et al. 1990; Mlot 1997; Gaze 2001; Nelson et al. 2002; MacAvoy et al. 2007). Phylogenetically, Rhynchocephalia is the sister taxon of Squamata (snakes, lizards, and amphisbaenians), and together both groups make up the larger group Lepidosauria (Figure 1), a monophyletic clade supported by a wealth of mor-

phological and molecular data (Evans 1984, 1988; Benton 1985; Schwenk 1986, 1988; Gauthier et al. 1988; Rieppel and deBraga 1996; deBraga and Rieppel 1997; Zardoya and Meyer 1998, 2001; Müller 2003; Rest et al. 2003; Townsend et al. 2004; Hill 2005). All lepidosaurs arose from a single common ancestor (independent of all other reptiles *sensu* Modesto and Anderson 2004; birds, crocodiles, turtles, and their fossil relatives), approximately 240-250 million years ago (Evans 2003; Vidal and Hedges 2005; unpublished data).

Sphenodon has long been of interest to anatomists because many aspects of its anatomy, including its muscles, were thought to demonstrate the ancestral condition for amniotes and/or diapsid reptiles (e.g., Byerly 1925; von Wettstein 1931, 1932, 1937; Anderson 1936; Sharell 1966; Barghusen 1973). Accordingly, it has been used in attempts to reconstruct the muscle arrangements

of several fossil amniotes including the phytosaur *Machaeroprotopus* (Anderson 1936) and the early synapsid *Dimetrodon* (Barghusen 1973). However, as Schwenk (1986, p. 148) has argued, the primitive nature of *Sphenodon* has previously been exaggerated. The absence of a tympanic membrane and distinctive physiology are probably both secondary features (Gans 1983; Whiteside 1986; Thompson and Daugherty 1992), and osteologically *Sphenodon* is certainly different from its well-known Mesozoic fossil relatives (e.g., Reynoso 2000; Apesteguía and Novas 2003; Jones 2008). Nevertheless, the phylogenetic position of *Sphenodon* as the only extant member of Rhynchocephalia means it is a potentially useful reference taxon for inferring soft tissue arrangement and structure in extinct animals, particularly when used in a phylogenetic bracket (e.g., Bryant and Russell 1992; Witmer 1995, 1997). It is also useful for evaluating the homology of muscles in extant taxa (e.g., Schwenk 1986; Holliday and Witmer 2007). Furthermore, understanding the muscle architecture in *Sphenodon* may provide clues as to why its close fossil relatives (other rhynchocephalians) demonstrate a variety of skull shapes that coincide with variation in tooth shape and tooth arrangement (Jones 2008).

The complete lower temporal bar means that *Sphenodon* is structurally analogous to the supposed ancestral condition (*Petralacosaurus*, Reisz 1977, 1981) of all diapsid reptiles (lepidosaurs, crocodiles, birds, etc.). Crocodiles and birds also demonstrate the diapsid condition but both are problematic as model organisms as crocodiles possess elongate rostra whereas birds have relatively large braincases and relatively small adductor chambers. It should be stressed, however, the lower temporal bar was absent in basal rhynchocephalians, such as *Gephyrosaurus* (Evans 1980), and has therefore been secondarily acquired in *Sphenodon* as repeatedly shown elsewhere (e.g., Whiteside 1983, 1986; Fraser 1988; Reynoso 2000; Evans 2003; Apesteguía and Novas 2003; Müller 2003; Wu 2003; Jones 2008). It is probably a structural feature for supporting the quadrate from joint reaction forces during biting and shearing (Whiteside 1983, 1986; Fraser 1988; Rieppel 1992; Wu 2003; Jones 2006a, 2008).

The arrangement of jaw and neck muscles dictates how an animal feeds and also how the skull is stressed during feeding. These, in turn, are likely to have a direct effect in forming the shape of the skull during growth (e.g., Gregory and Adams 1915; Adams 1919; Case 1924; Olson 1961;

Frazzetta 1968; Schumacher 1973a; Oxnard et al. 1995; Hunt 1998; Preuschoft and Witzel 2002; Witzel and Preuschoft 2005; Jones 2008). The muscle arrangement in *Sphenodon* is also of particular interest because it reflects a unique feeding mechanism among living organisms (Reilly et al. 2001). Following jaw closure the lower jaw moves forward (prorally) and shears food gripped by the teeth (Farlow 1975; Robinson 1976; Gorniak et al. 1982), allowing *Sphenodon* to deal with prey larger than its gape (Robinson 1973; Gorniak et al. 1982). Food items are also subjected to three-point bending because there is a row of teeth located on the lateral edge of the palatine bone parallel to the maxillary dentition (Evans 1980; Jones 2006a, 2007).

Many of the jaw muscles in *Sphenodon* have been described repeatedly (Byerly 1925; Lakjer 1926; Edgeworth 1935; Anderson 1936; Poglayen-Neuwall 1953; Ostrom 1962; Barghusen 1973; Haas 1973; Gorniak et al. 1982; Wu 2003; Holliday and Witmer 2007) but the accounts differ, and images are largely limited to lateral views of the skull. Descriptions of the tongue and associated throat muscles have also been made by several authors but are less common and in general are less detailed (e.g., Günther 1867; Lightroller 1939; Rieppel 1978; Schwenk 1986). Similarly the neck and pectoral muscles have arguably received less attention than the jaw muscles (Maurer 1896; Nishi 1916; Byerly 1925; von Wettstein 1931; Gasc 1981; Al-Hassawi 2004, 2007; Tsuihiji 2005, 2007). The osteology of *Sphenodon* has been described by many authors (e.g., Günther 1867; Siebenrock 1893, 1894; Werner 1962; Hoffstetter and Gasc 1969; Rieppel 1992; Evans 2008; Jones 2008).

The neck is widely recognised as an important part of an animal's feeding apparatus (e.g., Van Damme and Aerts 1997; Summers et al. 1998; Stevens and Parrish 1999; Upchurch and Barrett 2000; Rayfield et al. 2001; Anton et al. 2003; McHenry et al. 2007; Snively and Russell 2007ab). During feeding the positional relationship between the head and neck can change, as can be seen in tiger salamanders (*Ambystoma tigrinum*, Larsen and Guthrie 1975) and the Eastern box turtle (*Terrapene carolina*, Summers et al. 1998). This will probably affect the magnitude and distribution of strain and stress on the posterior regions of the skull. Most functional studies of skulls do not take into account the neck musculature, and when they do descriptions of its anatomy can be vague (e.g., McHenry et al. 2007). The tongue is also important in feeding. It is used to manipulate food items in the

mouth during processing (Walls 1981; Gorniak et al. 1982; Schwenk 2000; MEHJ pers. obs.), and several studies have observed that the tongue is also employed in pulling small prey into the mouth (e.g., Buller 1879; Gorniak et al. 1982; Schwenk 2000; pers. obs.), although Walls (1981, p. 91) did not observe this in the wild population he studied.

Sphenodon is carnivorous and opportunistic, feeding on a wide variety of arthropods, molluscs, and vertebrate material such as lizards, sea birds, and eggs (e.g., Günther 1867; Buller 1877, 1878; Reischek 1885; Dawbin 1949, 1962, 1982; Schmidt 1953; Farlow 1975; Walls 1981, 1982; Ussher 1999; Schwenk 2000). Examination of faecal pellets from Stephens Island (Walls 1981, 1982; Newman 1987) demonstrated that relatively slow terrestrial arthropods, such as the large darkling beetle (*Mimopeus opaculus*), were the most frequent prey items. Rare food items include hatchling *Sphenodon*, frogs, passerine birds and, on Green Island, the remains of crabs (Walls 1981; Newman 1987; Daugherty and Cree 1990; Blair et al. 2000; Moore and Godfrey 2006). Sea bird material is important (but not essential) to the larger stronger males on Stephens Island (Walls 1978, 1981; Cree et al. 1995a, 1999; Markwell 1998; Blair et al. 2000; Gaze 2001), particularly during spring and summer (Walls 1981). Females and juveniles may also consume more limited amounts of sea bird material but probably as carrion (Cree et al. 1995a).

Plant material is frequently present in *Sphenodon* faecal pellets (Walls 1981), and certain types of seeds have been found in almost 10% of scats examined as part of one study (I. C. Southey pers. comm. in Whittaker 1987). Although consumption of plant material may be accidental, it can represent 14% of the total number of items present in faeces (Walls 1981). This places *Sphenodon* within the generous omnivorous category of Cooper and Vitt (2002) (diet = >10% plant material). Many of the invertebrates and vertebrates that *Sphenodon* preys upon are also consumed by the Pacific rats (kiore, *Rattus exulans*). As a result, for populations of *Sphenodon* located on islands inhabited with Pacific rats, there is competition for food (Cree et al. 1995b; Blair et al. 2000).

Adult *Sphenodon* mainly hunt during the evenings (Walls 1981; Gans 1983; Daugherty and Cree 1990) because of their ability to be active in cool temperatures (Thompson and Daugherty 1998). They also possess large eyes that are sensitive to low light levels (Meyer-Rochow et al. 2005). Predation is mainly visual, and in most

cases is triggered by movement (e.g., Buller 1879; Farlow 1975; Walls 1981; Meyer-Rochow 1988; Meyer-Rochow and Teh 1991; Gorniak et al. 1982; Schwenk 2000) but taste buds are present on the tongue (Schwenk 1986) and consumption of eggs and carrion suggests that smell can also be involved (Walls 1981; see also Cooper et al. 2001). In terms of feeding strategy (*sensu* Pianka 1966; Huey and Pianka 1981), where “sit and wait” involves ambushing prey from a sedentary position and “widely foraging” involves actively hunting prey, *Sphenodon* is widely considered to follow a “sit and wait” strategy (e.g., McBrayer and Reilly 2002; Vitt et al. 2003). Nevertheless, Gans (1983) reported that *Sphenodon* may also inspect crevices for prey. Young tuatara are more active during the day, possibly to avoid predation from adults (Daugherty and Cree 1990), and this may influence the prey available to them. There is some evidence that they feed on smaller prey items (Ussher 1999, p.123).

The relationship between phenotype and diet remains poorly understood in lepidosaurs, leading some authors to question whether any predictable relationship exists at all (e.g., Schwenk 2000). Broadly comparative work (e.g., Metzger and Herrel 2005) is required in order to examine this relationship. It should be remembered, as in other lepidosaurs (e.g., Lappin and Husak 2005), *Sphenodon* also uses its jaws, teeth, and associated muscles in conspecific fighting for burrows, mates, and nesting sites (e.g., Newman 1987; Daugherty and Cree 1990; Gans et al. 1984; Gillingham et al. 1995; Nelson et al. 2004). Computer models as used by Moazen et al. (2008, 2009) can also provide biomechanical assessment of the hard and soft tissue structures involved and allow specific questions to be tested regarding the function of different anatomical components.

Here we provide a thorough review of *Sphenodon* osteology and muscle anatomy as relevant to feeding. We evaluate previous discrepancies and, for the first time, provide colour photographs and three-dimensional imaging to explain complex muscle arrangements. Our review will provide a basis for future work on muscular biomechanics during feeding.

OSTEOLOGY

The osteology of *Sphenodon* was first described in detail by Günther (1867) but numerous studies have been made subsequently. Because *Sphenodon* was once seen as a “basic” or “generalised” amniote, Romer (1956) used it as

his point of reference for a wide range of extinct and extant amniotes. Similarly, as the only extant rhynchocephalian, the skull of *Sphenodon* is often represented in text books (e.g., Kardong 1998, p. 250; Liem et al. 2001, p. 252). The skull structure of hatchling or near hatchling animals (skull length = 5–15 mm) was investigated by Howes and Swinnerton (1901), Werner (1962), and Rieppel (1992) whereas Osawa (1898) and, more recently, Evans (2008) described skulls of animals that were not fully grown. Ten skulls of different size were figured by Jones (2008), and geometric morphometrics showed that skull growth in *Sphenodon* is allometric because during ontogeny the postorbital part of the skull expands relative to the orbital and preorbital portions. Several descriptions have also been made of the braincase (Siebenrock 1893, 1894; Osawa 1898; Gower and Weber 1998; Evans 2008), the teeth (Gray 1831; Günther 1867; Colenso 1886; Harrison 1901ab; Howes and Swinnerton 1901; Robinson 1976; Throckmorton et al. 1981; Gorniak et al. 1982; Rieppel 1992; Jones 2006ab, in press), and the axial skeleton (e.g., Günther 1867; Howes and Swinnerton 1901; Hoffstetter and Gasc 1969). The cranial joints have been examined by Jones (2006a, 2007) but this will not be discussed in detail here.

The description that follows is based on previous literature but also from examination of numerous specimens from over a dozen collections:

- Auckland Museum, New Zealand (AIM).
- Berlin Museum of Natural History (Museum für Naturkunde) of the Humboldt-University, Germany (ZMB).
- Birkbeck College, School of Biological and Chemical Sciences, London, UK (BRK).
- Booth Museum of Natural History, Brighton, UK (BMB).
- Canterbury Museum, Christchurch, New Zealand (CMC).
- Ernst Moritz Arndt University of Greifswald, Zoology Collection, Germany.
- Grant Museum of Zoology, UCL, London, UK (LDUCZ).
- Huntarian Museum and Art Gallery, University of Glasgow, UK (GLAHM).
- Kings College London, Life Sciences, London, UK (KCL).
- The Manchester Museum, University of Manchester, Manchester, UK (MANCH).
- Natural History Museum, London, UK (BMNH).
- Oxford Museum of Natural History, Oxford, UK (OUMNH).
- David Gower Personal Collection, NHM, UK (DGPC).
- University Museum of Zoology, Cambridge, UK (UMZC).
- The Field Museum, Chicago, USA (FMNH).
- Museum of New Zealand Te Papa Tongarewa (Wellington), New Zealand (NMNZ).
- University of Auckland, New Zealand (AU).

The skull of an adult *Sphenodon* possesses a short snout, large orbits, and a relatively large postorbital area (Figure 2), and is, in general, approximately 60 mm long from the tip of the rostrum to a point level with the jaw joints (Günther 1867; Jones 2008). The lacrimal bone is absent (*contra* Günther 1867 and Anderson 1936) in contrast to many squamates where it borders the anterior part of the orbit (e.g., Jollie 1960; Gauthier et al. 1988; Evans 2008). Correspondingly, in *Sphenodon* the lacrimal canal runs between the prefrontal and maxilla (Figure 2.1). Note that the term ‘lacrimal canal’ is still used despite there being no lacrimal gland (e.g., Underwood 1970). Above the tooth row is a band of hard tissue referred to here as secondary bone (Harrison 1901ab; Jones 2006ac), and the jaw joint is situated ventral to the long axis of the tooth row (Jones 2008). Both lower and upper temporal fenestrae are present and bounded by lower and upper temporal bars (Günther 1867). The former is composed of the postorbital and squamosal (“mastoid” of Günther 1867; Osawa 1898) whereas the latter is composed primarily of the posterior process of the jugal (“zygomatic” of Günther 1867) with smaller contributions from the squamosal and quadratojugal. In contrast to the prevalent view, current evidence indicates that the lower temporal bar in *Sphenodon* has been secondarily acquired and does not represent the plesiomorphic condition for lepidosaurs (Whiteside 1983, 1986; Fraser 1988; Rieppel 1993; Reynoso 2000; Apesteguía and Novas 2003; Müller 2003; Wu 2003; Evans 2003, 2008; Jones 2006ac, 2008; *contra* Herrel et al. 1998, 2007; Kardong 1998, p. 249; Hildebrand and Goslow 2001, p. 129; Liem et al. 2001, p. 90; Pough et al. 2005, p. 343).

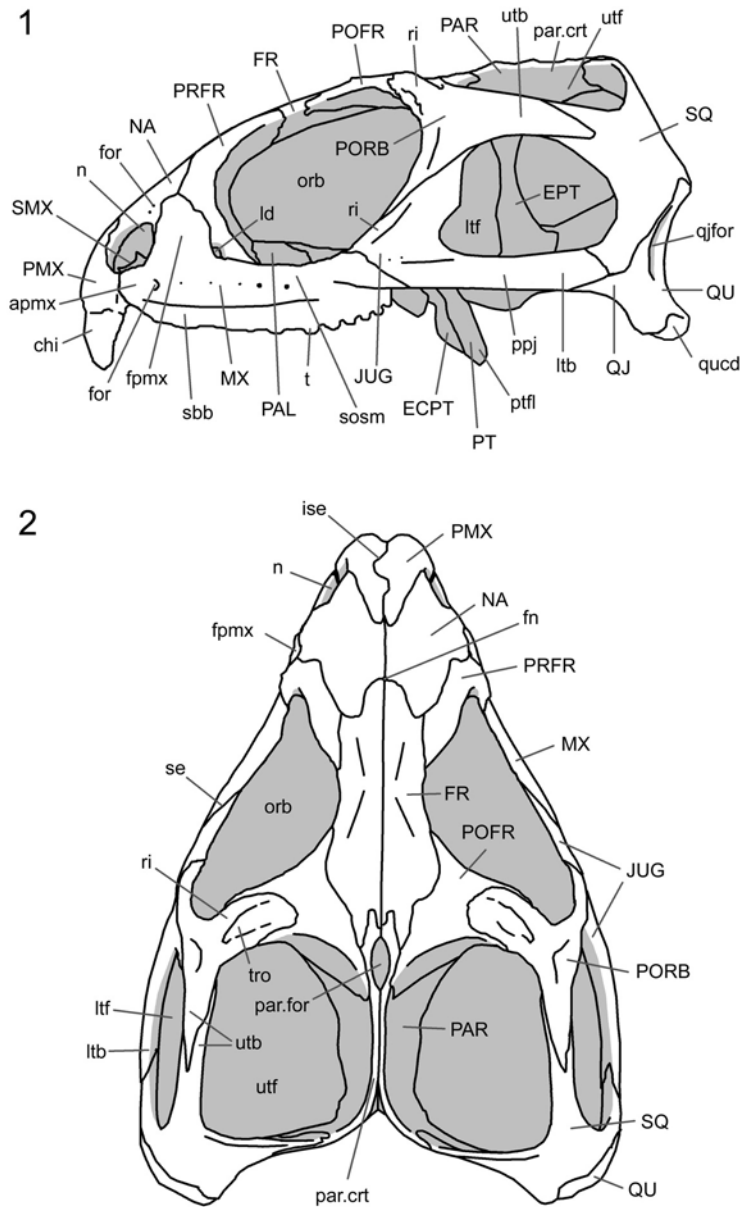


FIGURE 2. Skull of *Sphenodon*. 2.1 lateral view (specimen OMNH 908). 2.2 Dorsal view (NMNZ RE0385). Skull length approximately 60mm. Please see Abbreviation Appendix for anatomical abbreviations.

Premaxillae, nasals, frontals, and parietals are paired although the seam between the parietals can be indistinct posteriorly (Figure 2.2; Günther 1867; Siebenrock 1893, 1894; Jones 2006a). Anteriorly the seam is interrupted by a lenticular parietal foramen (Günther 1867). In life this accommodates the so-called third-eye (Dendy 1911; Robb 1977). In adults the medial edges of the parietal combine to form a crest (Günther 1867; Jones 2008), and the posterolateral margins slope ventrolaterally to form a shelf. The posterolateral process interlocks with the medial process of the squamosal to create

a posterior temporal bar. Supratemporal bones are absent (but see Rieppel 1992).

In about 25% of the specimens examined ($n = 40$) (e.g., *Sphenodon* specimens BMNH1844.102911, MANCH C.1206.49, KCL x12, LDUCZ x146; Jones 2006a) a small fontanelle is present at the junction between the nasals and frontals. The postfrontals are relatively large compared to fossil rhynchocephalians (Jones 2006a) and meet the parietals and frontals medially (Günther 1867). Laterally the postfrontals interlock with the postorbitals (Jones 2006a). The latter

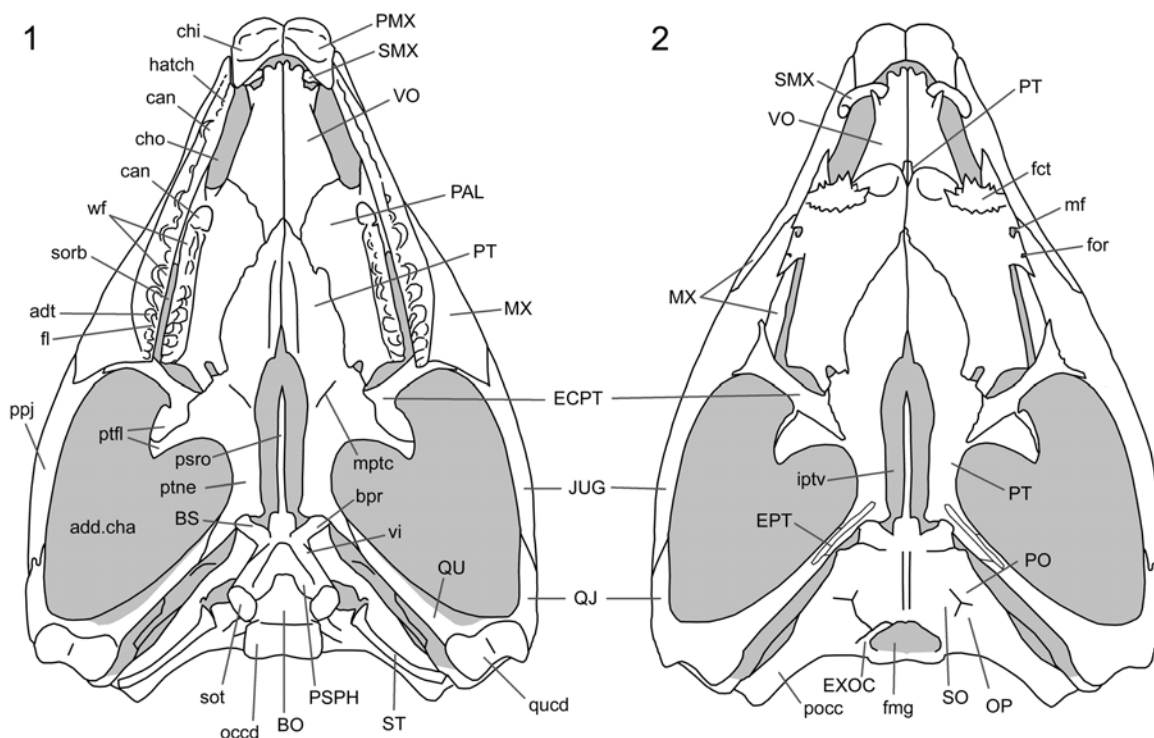


FIGURE 3. Skull of *Sphenodon* (NMNZ RE0385). 3.1 Ventral view 3.2 Dorsal view of the palate. Right jugal-quadratojugal seam modified to reflect intraspecific variation (e.g., DGPC1). Skull length approximately 60 mm.

bone is a triradiate element that bears a trough on its dorsal surface bounded by two ridges running oblique to the midline axis (Jones 2006a). The strength of the trough and ridges varies intraspecifically, usually (but not always) being better defined in larger skulls (Jones 2006a).

The dorsal portion of the braincase is composed of the prootic, opisthotic, and supraoccipital bones. The supraoccipital bears a posterodorsally projecting crest (“crista supraoccipitalis” of Siebenrock 1894, p. 310). Ventral to this is the foramen magnum, which is laterally bounded by the exoccipitals. More lateral still, the paroccipital processes of the opisthotics extend towards the posteromedial bases of the squamosals (Gower and Weber 1998) (Figure 3, 4).

The palate of *Sphenodon* is vaulted and composed of paired vomers, palatines, and pterygoids (Figure 3.1). All of these bones meet in the midline as visible in dorsal view (Figure 3.2). A lateral process of the pterygoid and ventral process of the ectopterygoid contribute to a substantial pterygoid flange (Günther 1867; Jones 2006a). The posterior process of the pterygoid laps the medial surface of the quadrate forming a dorsoventrally deep quadrate-ptyergoid wing (Günther 1867; Jones 2006a). Against the lateral surface of the pterygoid, and

adjacent to the anterior edge of the quadrate, sits a broad based epipterygoid (“columella” of Günther 1867).

The lower jaw is robust and has a conspicuous mandibular foramen (Günther 1867; Osawa 1898; Baur 1891; Throckmorton et al. 1981). The dentary extends posteriorly to a point level with the articular surface (Figure 5). Posterior to the tooth row the dentary also expands dorsally into the coronoid process (cpd = coronoid process of the dentary, Jones 2006c) and braces the coronoid bone. The latter is large and contacts both the prearticular and angular ventrally. Note that the angular bone was described and labelled as a splenial bone by early authors (e.g., Günther 1867; Osawa 1898, Baur 1891). The dorsal surface of the articular is saddle-shaped and expanded antero-posteriorly to be about two and a half times the length of the bi-lobate articular surface of the quadrate (e.g., DGPC2). Pathologies on the lower margin of the lower jaw are not infrequent (e.g., Figure 6; BMNHD.405; LDUCZ x036, LDUCZ x146; LDUCZ x343; KCL X12; Robb 1977, figure 5) and probably result from infections following injuries sustained during fighting with conspecifics (Evans 1983; Daugherty and Cree 1990). On the labial surface of the dentary below the tooth row a skirt of second-

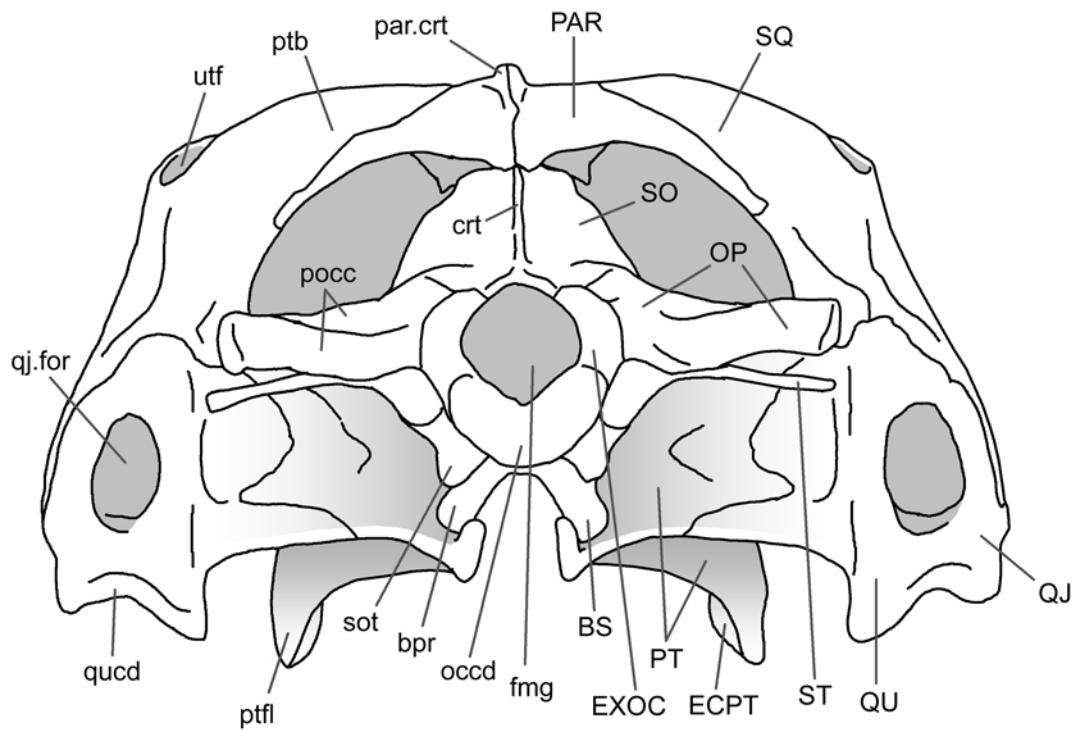


FIGURE 4. Occipital view of *Sphenodon* (YPM9194). Skull length approximately 60 mm.

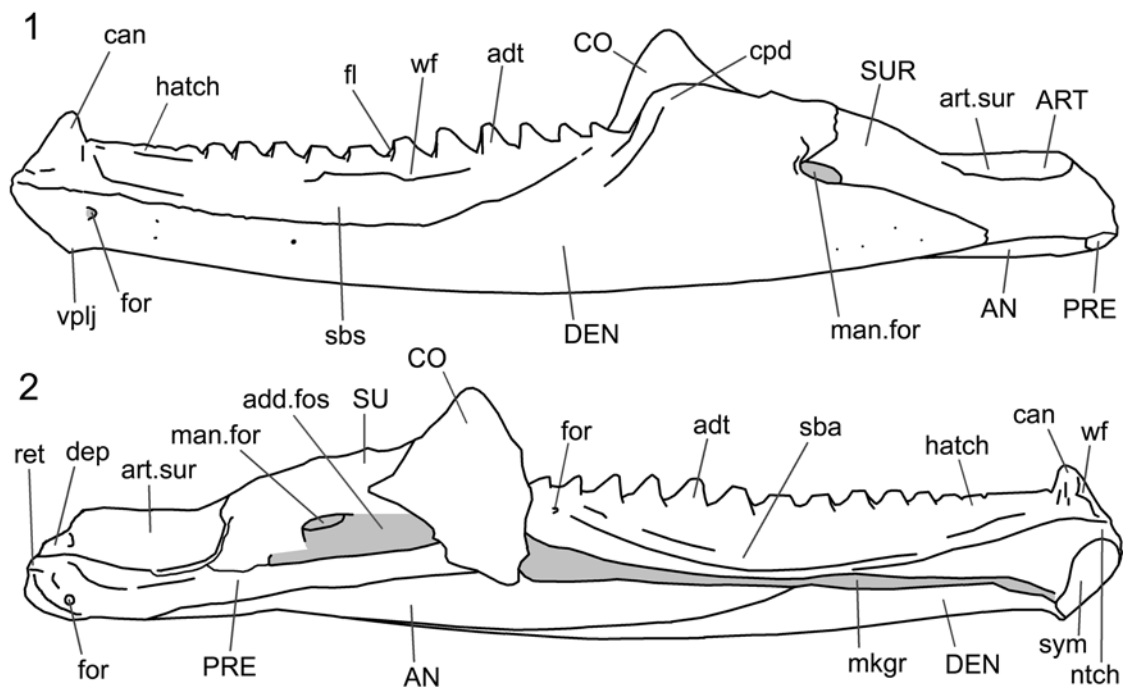


FIGURE 5. Lower jaw of *Sphenodon* (LDUCZ x721 right side flipped [reversed]). 5.1 Labial view. 5.2 Lingual view. Jaw length approximately 55 mm.

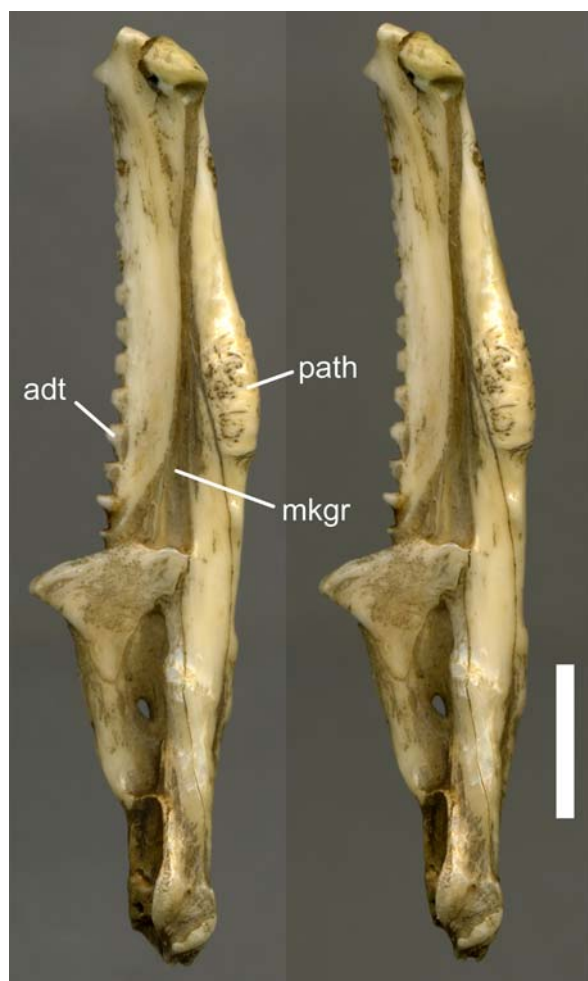


FIGURE 6. Lingual view stereopair of a left *Sphenodon* lower jaw (LDUCZ x343). Scale equals 10 mm.

ary bone develops ontogenetically. This bony skirt has an obvious ventral edge in adults (Harrison 1901ab; Jones 2006a) and compensates for wear from the maxillary teeth (Robinson 1976; Fraser 1988). The additional bone also strengthens the lower jaw by increasing its cross-sectional area (Jones 2006a). On the lingual surface is a more planar apron of secondary bone. The symphyseal surface is comma-shaped, generally smooth, and located ventral to a notch that has also been found in some fossil rhynchocephalians (Evans et al. 2001). In life the symphysis is maintained by a fibrous ligament that permits some accommodating movement between the left and right lower jaws (Figure 7) (Günther 1867, p. 600; Robinson 1976, p. 54; Schwenk 2000, p. 189).

The teeth of *Sphenodon* are fused to the crest of the jaw bone with an acrodont implantation (Günther 1867; Robinson 1976; Augé 1997; Kieser et al. 2008). In adults the premaxilla bears a single

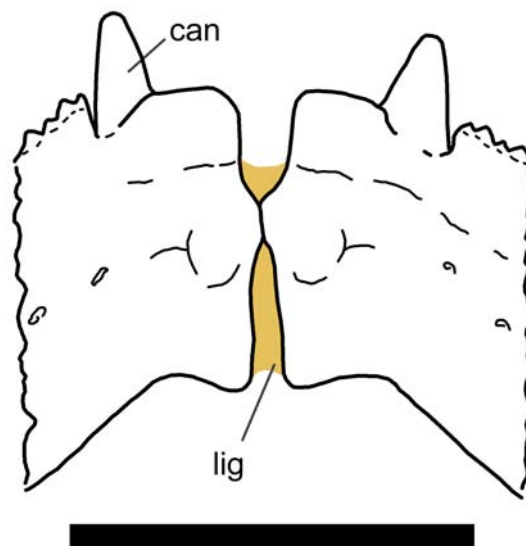


FIGURE 7. Anteroventral view of the symphysis in *Sphenodon* redrawn from Robinson (1976). Scale equals 10 mm.

large chisel-like tooth bearing two cusps that when worn can superficially resemble the incisor tooth of some mammals (Günther 1867; Newman 1878; Howes and Swinnerton 1901; Robinson 1976). It changes ontogenetically as hatchlings possess three distinct teeth (Günther 1867; Howes and Swinnerton 1901; von Wettstein 1931; Werner 1962; Rieppel 1992). The anterior part of the maxillary tooth row comprises a set of hatchling teeth that alternate in size (Harrison 1901ab; Howes and Swinnerton 1901; Werner 1962; Robinson 1976; Rieppel 1992; Reynoso 2003). This can be so highly worn in adults that individual teeth are not discernable. Some of the hatchling teeth are also replaced by secondary teeth or caniniforms (Robinson 1976; Reynoso 2003). The more posteriorly situated dentition consists of adult (or “additional”) teeth individually added to the rear of the tooth row during ontogeny. These teeth are larger than the hatchling teeth. They are conical and stout but with a worn medial surface and a posterolingually directed flange (Robinson 1976; Throckmorton et al. 1981; Gorniak et al. 1982; Rieppel 1992; Jones 2006a).

A large row of teeth is present on the lateral margin of the palatine nearly parallel to the teeth on the maxilla (Figure 3.2) so that the dentary teeth fit between the two upper rows when the jaws close. The enlarged palatine tooth row is something Gray (1831) noted in the first description of *Sphenodon* (incorrectly identified as an agamid) and represents a unique feature of Rhynchocephalia

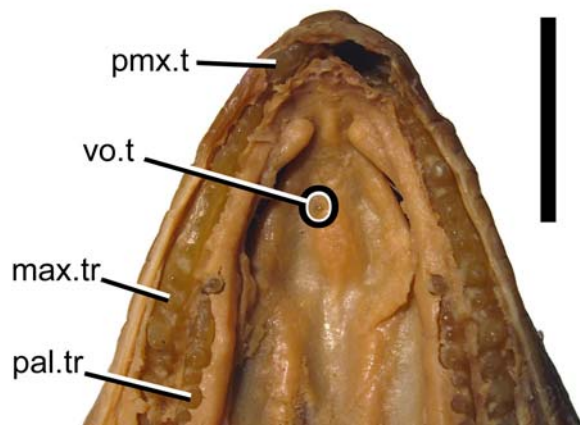


FIGURE 8. Vomerine tooth visible in *Sphenodon* specimen BMNH 1972.1223. Scale equals 10 mm.

amongst extant amniotes (Evans 2003; Jones 2007). The teeth on the palatine are to some extent mirror images of those on the maxilla: conical and stout but with a worn lateral surface and a postero-labial directed flange. Anteriorly juveniles possess a row of hatchling dentition that alternates in size (e.g., OUMNH 700) whereas adults possess a conical caniniform (Robinson 1976; Jones 2006a). A vestigial tooth may be found on each of the vomers in juveniles and occasionally in adult individuals of *Sphenodon* (e.g., specimens AMPC1, LDUCZ x1176 (previously referred to as x804), UCLGMZ x343, BMB100225, OUMNH 4911). Howes (1890) and Harrison (1901a, p. 162) did not think these teeth ever entered the oral cavity, but Siebenrock (1894, p. 310) observed that the teeth of dry specimens were long enough to do so. Examination of specimen BMNH 1972.1223 confirms the suggestion of Siebenrock (1893, 1894) (Figure 8).

The dentary teeth almost invariably demonstrate wear, particularly on their labial and lingual surfaces (Robinson 1976; Reynoso 1996). The majority of teeth on the dentary are pyramidal with an anteriorly positioned apex that possesses anterolingual and anterolateral flanges (Robinson 1976; Throckmorton et al. 1981; Gorniak et al. 1982; Jones 2006ab, 2008, in press, Jones et al., 2009). However, as for the maxilla and palatine, there is a set of hatchling teeth anteriorly. Again this can be obscured or obliterated by wear in adults and is usually partially replaced by a conical caniniform tooth (Harrison 1901ab; Howes and Swinnerton 1901; Robinson 1976; Reynoso 2003). The antero-dorsal tip of each lower jaw may bear an oblique wear facet from where it impacts the back of the corresponding chisel-like premaxillary tooth during

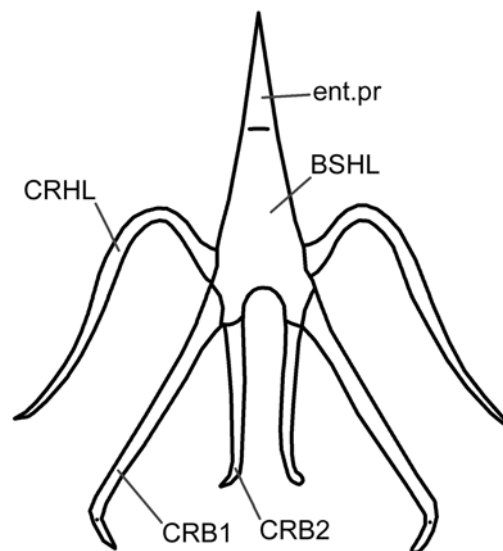


FIGURE 9. The hyobranchial skeleton of *Sphenodon*. Redrawn from Osawa 1898.

the prooral jaw shearing (e.g., OMNH 908; OMNH 4911; Jones 2006a).

The hyobranchial skeleton is a remnant of the visceral skeleton (splanchnocranium) and is associated with the tongue and throat muscles. The structure in *Sphenodon* has been described several times (e.g., Osawa 1898; Fürbringer 1922; von Wettstein 1931, 1932; Romer 1956; Tanner and Avery 1982). It comprises a relatively broad midline basihyal composed of cartilage (Figure 9). The basihyal has three anterior projections, of which the median entoglossal process supports the tongue. The two shorter anterolateral processes are connected to a pair of long thin ceratohyals that curve dorsolaterally around the pharynx. Extending posterolaterally from the central body of the basihyal are two pairs of projections: the bony first ceratobranchials, and the shorter and more medially located second ceratobranchials (Osawa 1898; Fürbringer 1922; Rieppel 1978; Tanner and Avery 1982). Comparison of previous illustrations (e.g., Osawa 1898; Fürbringer 1922; Edgeworth 1935; Rieppel 1978; Tanner and Avery 1982) suggests that there may be some intraspecific variation in the length of different components.

The skull and neck are connected by the atlanto-occipital joint which involves both the first and second vertebrae (atlas and axis respectively) (axis = epistropheus of Günther 1867, Osawa 1898 and Nishi 1916) (Figure 10). Also between the occiput and atlas are two small triangular proatlantes (Howes 1890). The atlas consists of an inter-centrum and the two halves of the neural arch that

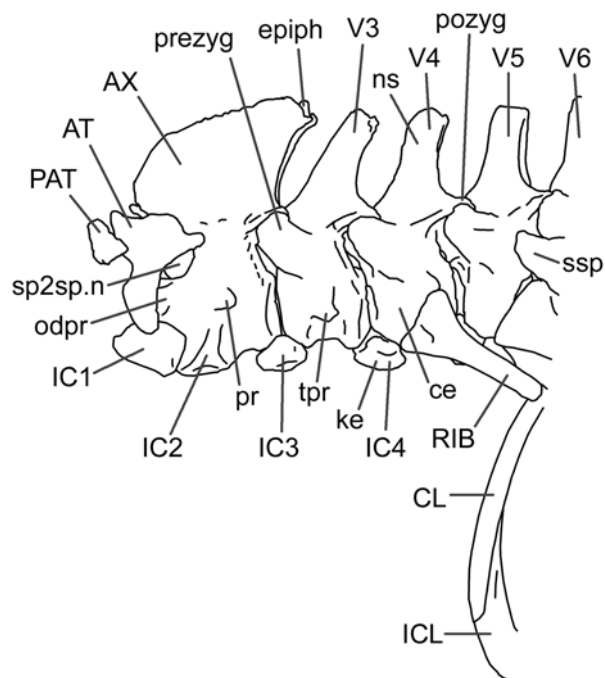


FIGURE 10. Neck osteology in *Sphenodon* (YPM 9194). The third vertebral centrum is approximately 5 mm long.



FIGURE 11. The atlas and axis of *Sphenodon* in anterior and left lateral view (specimen LDUCZ x722). Note the dorsal edge of the axis neural spine is damaged. Scale equals 1 mm.

extend posteriorly to a zygapophysial joint with the anterodorsal surface of the atlas (LDUCZ x722, LDUCZ x723). The atlas centrum is fused to the axis centrum to form the odontoid process which, in conjunction with the first intercentrum and neural arch bases provides a wide cup-like socket for the ovoid basioccipital condyle (Figures 11 and 12).

The neural spine of the heavily-built axis is greatly expanded antero-posteriorly (Günther 1867; von Wettstein 1931). The small axis transverse processes are very small and do not bear ribs in adults. The second intercentrum is fused to the axis centrum in adults (Hoffstetter and Gasc 1969; e.g., specimens LDUCZ x036, LDUCZ x723), to form a large saddle-like anterior surface



FIGURE 12. Stereopair showing the occipital condyle of *Sphenodon* in posterior view (specimen is from David Gower's personal collection [DGPC2] and was also featured in Gower and Weber 1998). The posterior temporal bars have been removed as well as part of the left pterygoid.

which is convex in the horizontal plane and concave in the vertical plane (Günther 1867, figure 18). This articulates with the atlas intercentrum and allows some rotational movement between the two bones.

Post-axis cervical vertebrae (V3-8) possess a centrum that is cylindrical, notochordal (amphicoelous), has a medioventral ridge, and has expanded anterior and posterior ends (Günther 1867; Hoffstetter and Gasc 1969). The neural arches bear tall neural spines and anterior and posterior zygapophyses (Figure 10) that have a mainly dorso-ventral articulation but there are also small incipient zygosphenes-zygantrum joints medially (Hoffstetter and Gasc 1969, p. 237; Gauthier et al. 1988). Laterally short transverse processes articulate broadly with deep headed ribs (Günther 1867; Hoffstetter and Gasc 1969).

Typically the first ossified rib is attached to the fourth vertebra (Hoffstetter and Gasc 1969) (although part of a double headed rib can be seen in specimen LDUCZ x036 attached to the third vertebra). The rib of the fourth vertebra is small and may be double headed (Hoffstetter and Gasc 1969), single headed (e.g., LDUCZ x036), or may bear a double headed rib on one side only (e.g., YPM 9194; LDUCZ x722). The first ossified rib may also articulate with the intercentrum (Hoffstetter and Gasc 1969; Al-Hassawi 2004, 2007). The ribs of vertebrae 5, 6, and 7 are also short but have expanded distal ends partly made of cartilage. The rib of the 8th vertebra is long but does not contact the sternum as do the ribs of vertebrae 9 to 12 (Hoffstetter and Gasc 1969). Extending between the ventral surfaces of postaxial vertebrae are smaller intercentra, some of which possess a ven-

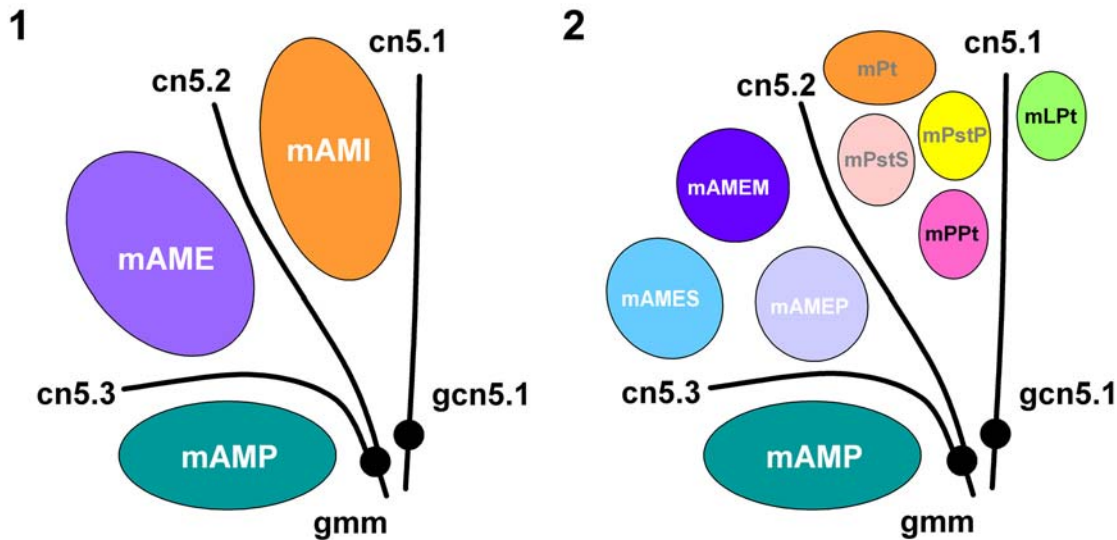


FIGURE 13. Schematic diagram of the adductor chamber in left dorsal view showing the relative positions of muscles and divisions of the trigeminal nerve (cn5). 13.1 Major muscle compartments defined by their positions relative to the trigeminal divisions. 13.2 Individual muscles within each compartment. Redrawn from Haas (1973) and Holliday and Witmer (2007).

tral midline keel (Hoffstetter and Gasc 1969; Al-Hassawi 2004, 2007).

In adults the pectoral girdle is composed of paired scapulocoracoids, paired clavicles and, ventrally, a slender T-shaped interclavicle (Günther 1867; Osawa 1898; Fürbringer 1900; Howes and Swinnerton 1901; von Wettstein 1931). Extending from the dorsal edges of the scapulocoracoids are relatively short cartilaginous suprascapulae. Each clavicle attaches to the anterior edge of the scapulocoracoid dorsal to a subtle embayment (Howes and Swinnerton 1901; Osawa 1898). Medially each clavicle overlaps the anterior edge of the interclavicle (LDUCZ x036, LDUCZ x722).

MUSCULATURE

The musculature of *Sphenodon* has been described by a number of authors including Osawa (1898), Nishi (1916), Byerly (1925), Lakjer (1926), Edgeworth (1935), Poglayen-Neuwall (1953), Romer (1956), Ostrom (1962), Rieppel (1978), Gorniak et al. (1982), Schwenk (1986), Wu (2003), Al-Hassawi (2004, 2007), and Tsuihiji (2005, 2007). However, a full review of the muscles involved in feeding, including those of the neck, has not previously been attempted. To confirm previous reports and gather new data, several partially dissected specimens (Table 1) were examined using a Wild Stereo microscope and drawn using a *camera lucida*.

THE TRIGEMINAL MUSCLES

This section describes the muscles of the skull innervated by the trigeminal nerve (cranial nerve 5 [cn5]). The divisions of the trigeminal nerve (cn5) have long been used to infer the homology of muscular units in the adductor chamber (Luther 1914; Lakjer 1926; Oelrich 1956; Ostrom 1962; Barghusen 1973; Haas 1973; Gomes 1974; Schwenk 2000; Holliday and Witmer 2007). The trigeminal nerve branches anteriorly into the ophthalmic division (cn5.1), anterolaterally into the maxillary division (cn5.2) and laterally into the mandibular division (cn5.3). The muscle tissue between the mandibular division (cn5.3) and the maxillary division (cn5.2) is referred to as the m. Adductor Mandibulae Externus (mAME); the muscle posterior to the mandibular division (cn5.3) is referred to as the m. Adductor Mandibulae Posterior (mAMP); and the muscle between the ophthalmic division (cn5.1) and maxillary division (cn5.2) is grouped as the m. Adductor Mandibulae Internus (mAMI) (Figure 13).

Most of the muscles innervated by the trigeminal nerve comprise the main jaw adductor muscles. These have repeatedly been described in varying degrees of detail (Osawa 1898; Byerly 1925; Lakjer 1926; Edgeworth 1935; Lightroller 1939; Anderson 1936; Poglayen-Neuwall 1953; Ostrom 1962; Barghusen 1973; Haas 1973; Gorniak et al. 1982; Wu 2003; Holliday and Witmer

TABLE 1. Wet material examined.

Specimen	Skull length	Description
BMNH 1972.1.22.3	40 mm	Most muscles still intact but cut horizontally at the level of the coronoid (presumably to inspect the interior of the mouth and/or cross-sectional areas of the muscles). Detail of the m. Depressor Mandibulae is also visible.
BMNH1922.6.16.2	64 mm	Very little of the jaw muscles remains but fascia is still present in the lower temporal fenestra.
BMNH 1969.2204	62 mm	Adductor muscles dissected on left side. The right side of the neck has been partially dissected. It may be the specimen referred to by Haas (1973) and is probably the specimen used by Al-Hassawi (2004, 2007)
FMNH 270560	both around 60 mm long	Two <i>Sphenodon</i> heads partially dissected. Once belonged to Professor Carl Gans. Possibly referred to as CG 5369 and CG 5370 by Gorniak et al. (1982).

2007). Byerly (1925), Gorniak et al. (1982), Ostrom (1962), Haas (1973), and Wu (2003) report having dissected two specimens whereas Barghusen (1973) examined one. The account of Anderson (1936) seems largely to be a translation of Lakjer (1926). Holliday and Witmer (2007) also rely on previous literature but did dissect a range of other amniotes including several squamates. Similarly, Abdala and Moro (2003) coded the cranial muscles of *Sphenodon* for a cladistic analysis of lepidosaurs based on previous descriptions (citing Lakjer [1926] and Haas [1973]) and their knowledge of squamate muscles.

Remaining muscles innervated by the trigeminal nerve include the m. Constrictor Internus Dorsalis and the m. Constrictor Ventralis Trigemini (Haas 1973).

m. Adductor Mandibulae Externus (mAME)

This is an important muscle group used for applying hard bites when the jaws are nearly closed because it is at this point that most of the muscle fibres are orientated perpendicular (orthogonal) to the long axis of the tooth rows (Byerly 1925; Gorniak et al. 1982; Jones 2008). The mAME is subdivided into three portions: the superficialis, medialis, and profundus (Lakjer 1926). In general the muscles originate from the lateral surface and dorsal margins of the adductor chamber. The medialis and profundus attach to an aponeurosis (basal aponeurosis or bodenaponeurosis of Lakjer [1926] and Anderson [1936]), a tendinous sheet that extends from the dorsal margins of the surangular and coronoid bones, with the medialis inserting on its lateral surface and the profundus inserting on its medial surface.

Some of the origins of the external adductor muscles as figured by Holliday and Witmer (2007, p. 7, figure 4A) for *Sphenodon* do not correspond to previous descriptions. Moreover, as labelled, the deep muscles (m. Adductor Mandibulae Externus Profundus [mAMEP]) are reported as originating superficially to more superficial muscles (m. Adductor Mandibulae Externus Medialis [mAMEM]).

m. Adductor Mandibulae Externus Superficialis (mAMES). Following Haas (1973, p. 196), Wu (2003) divided the m. Adductor Mandibulae Externus Superficialis into three portions: the m. Levator anguli oris (mLAO), m. Retractor anguli oris (mRAO), and the m. Adductor Mandibulae Externus Superficialis *sensu stricto* (mAMESs). For lepidosaurs, Lakjer (1926) refers to the first two subunits (mLAO + mRAO) as Part 1a and the third (mAMESs) subdivision as Part 1b. This terminology was also used by Rieppel and Gronowski (1981).

The m. Levator Anguli Oris is generally present in squamates but not in crocodiles or birds (Haas, 1973). In *Sphenodon*, Haas (1973) described it as “complex” whereas Wu (2003, p. 590) described it as a strap-shaped muscle that originates from the medial surface of the postorbital near the postorbital-postfrontal joint via “a weak tendon.” It has a near vertical path and inserts on the anteromedial surface of the dorsal margin of the rictal plate (“Mundplatte”), part of a tendinous sheet that is visible at the angle of the mouth and attached to the overlying skin (Oelrich 1956; Wu 2003). This corresponds closely to the descriptions of Haas (1973, p. 293) and Gorniak et al. (1982, figures 1 and 2). Abdala and Moro (2003) code this muscle as being narrow and triangular

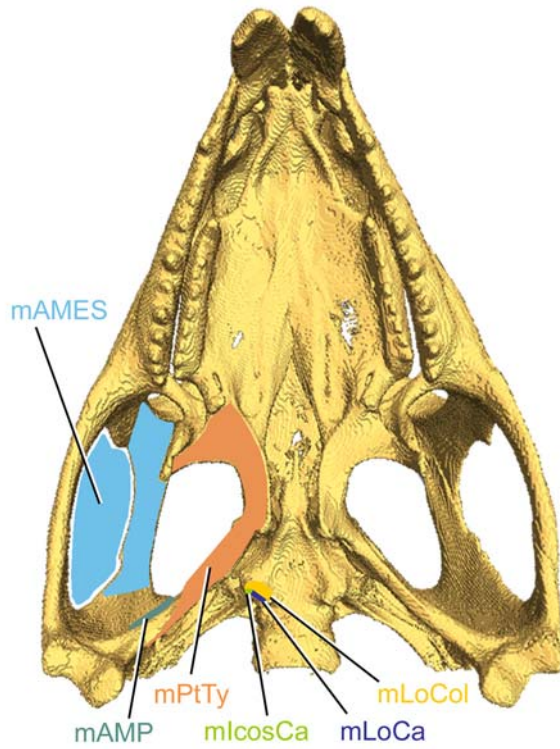


FIGURE 14. Skull model of *Sphenodon* (LDUCZ x036), based on micro CT data, in ventral view labelled with the areas of muscle attachment. Colour coding broadly follows that of Holliday and Witmer (2007) and is used here throughout.

without an origin on the jugal. Elsewhere the muscle is described as originating from the fascia of the lower temporal fenestra and/or from the lower temporal bar (Poglayen-Neuwall 1953; Rieppel and Gronowski 1981). Neither Lakjer (1926) nor Byerly (1925) described this muscle in *Sphenodon*.

The m. Retractor Anguli Oris (mRAO) is thin, triangular, and mainly originates as a sheet-like tendon from the descending process of the squamosal (Haas 1973; Wu 2003), although some fibres may arise directly from the posteroventral corner of the lower temporal fenestra at the squamosal-quadratojugal joint (Haas 1973; Wu 2003). The muscle attaches to the dorsalmost margin of the lateral rictal plate after following an anteroventral path (Haas 1973; Wu 2003). This muscle does not originate from the lower temporal bar.

The m. Adductor Mandibulae Externus Superficialis (mAMES) *sensu stricto* is thought to have been small in early amniotes (Heaton 1979; Rieppel and Gronowski 1981) but it can be very well developed in squamates (Haas 1973; Gomes 1974; Rieppel and Gronowski 1981). According to Wu (2003), the m. Adductor Mandibulae Externus Superficialis (mAMES) *sensu stricto* may be further divided into an anterolateral component and a smaller posteromedial component. Gorniak et al. (1982) made a similar, but not necessarily equivalent division (e.g., Gorniak et al. 1982, table 1) based on differences in fibre length.

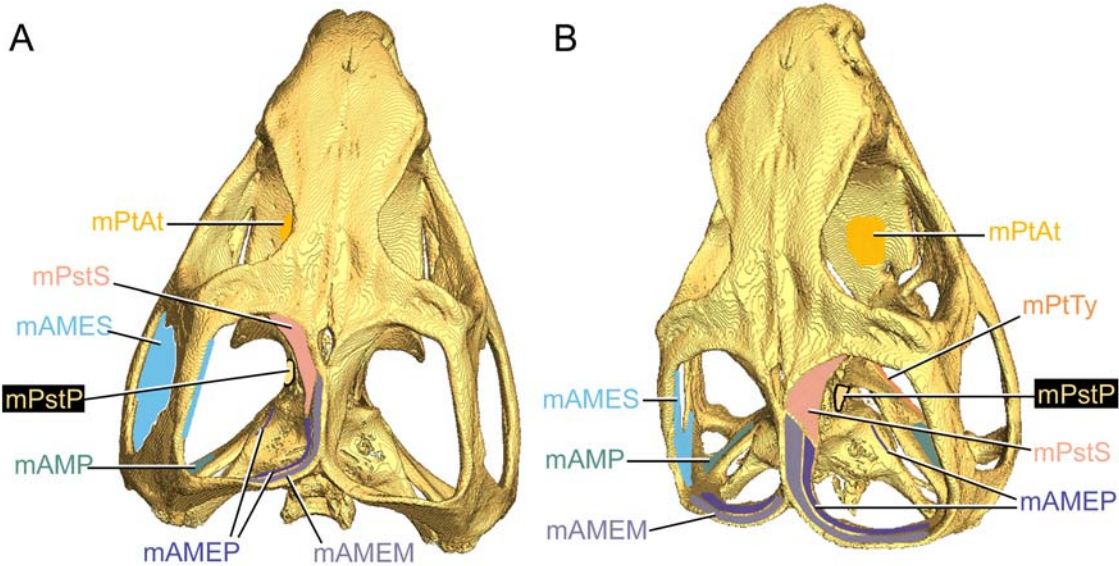


FIGURE 15. Skull model of *Sphenodon* (LDUCZ x036), based on micro CT data, labelled with the areas of muscle attachment. A: Dorsal view. B: Dorsolateral view.

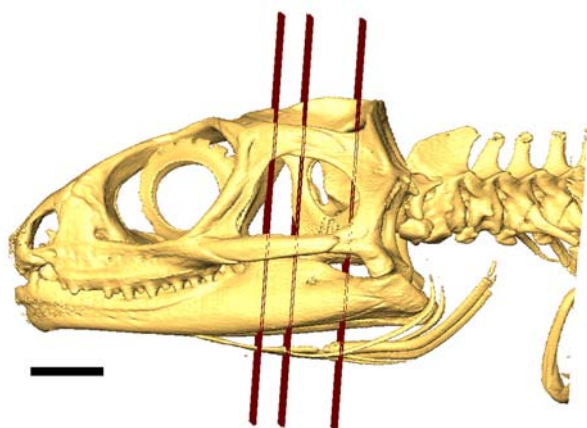


FIGURE 16. Skull model of *Sphenodon* (YPM 9194), based on micro CT data, in left lateral view demonstrating the location of the schematic coronal cross-sections shown in Figure 17.

The muscle originates from the fascia of the lower temporal fenestra and also directly from the medial surface of the upper temporal bar (postorbital+squamosal), the neighbouring edges of the squamosal, and the posteromedial surface of the postorbital bar (jugal+postorbital) (Figures 14, 15, 16, 17, 18, 19, 20, 21, 22, and 23) (Edgeworth 1935; Anderson 1936; Poglayen-Neuwall 1953; Haas 1973; Gorniak et al. 1982; Wu 2003). The presence of a thin but strong fascia (“Sehnenplatte” of Poglayen Neuwall 1953) that provides an attachment surface for the mAMES was confirmed by direct examination of specimens (e.g., left side of BMNH 1922.6.16.2, right side of FMNH 270560 skull, right side of BMNH 1969.2204) (Figure 20). Otherwise the attachment to the medial surface of the postorbital bar is fleshy (Haas 1973). When the jaws are closed the fibres are oriented with a near perpendicular angle to the long axis of the lower jaw (Haas 1973; Wu 2003). Note that Haas (1973) and Lakjer (1926) both considered fibres arising from the medial surface of the upper temporal bar to be part of the mAMEM rather than the mAMES. Their distinction was made because they define the mAMES as only comprising fibres arising from the fascia of the lower temporal fenestra.

Insertion occurs extensively on the lateral surface of the lower jaw: namely the lateral surface of the dentary, lateral surface of the coronoid bone, and lateral surface of the surangular (Figures 16, 17, 21, 23, 24 and 25; Anderson 1936; Rieppel and Gronowski 1981; Gorniak et al. 1982). According to some authors, a subset of deep fibres may also attach on the lateral surface of the basal aponeurosis (Haas 1973; Wu 2003). Examination of speci-

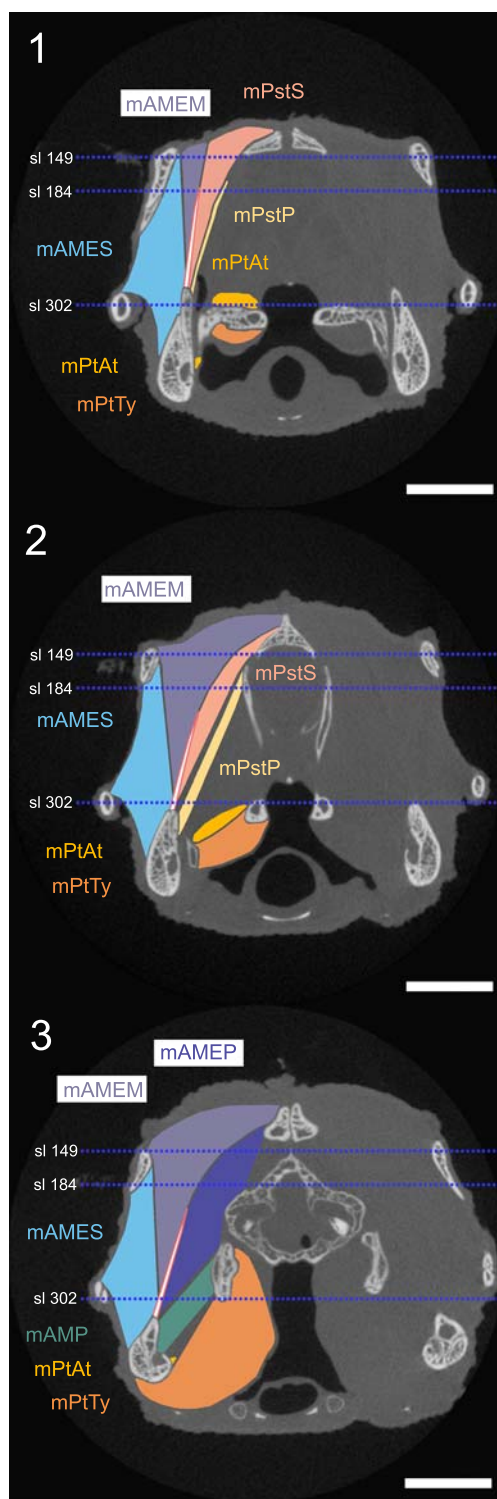


FIGURE 17. Coronal CT slices (YPM 9194) with schematic representations of the muscles and basal aponeurosis added. 17.1 Slice 235, near the tallest point of the coronoid bone. 17.2 Slice 261 through the anterior edges of the epipterygoids. 17.3 Slice 309 through the posterior portion of the postorbital bone. Locations of the horizontal slices (see below) are shown in blue. Scale equals 10 mm.

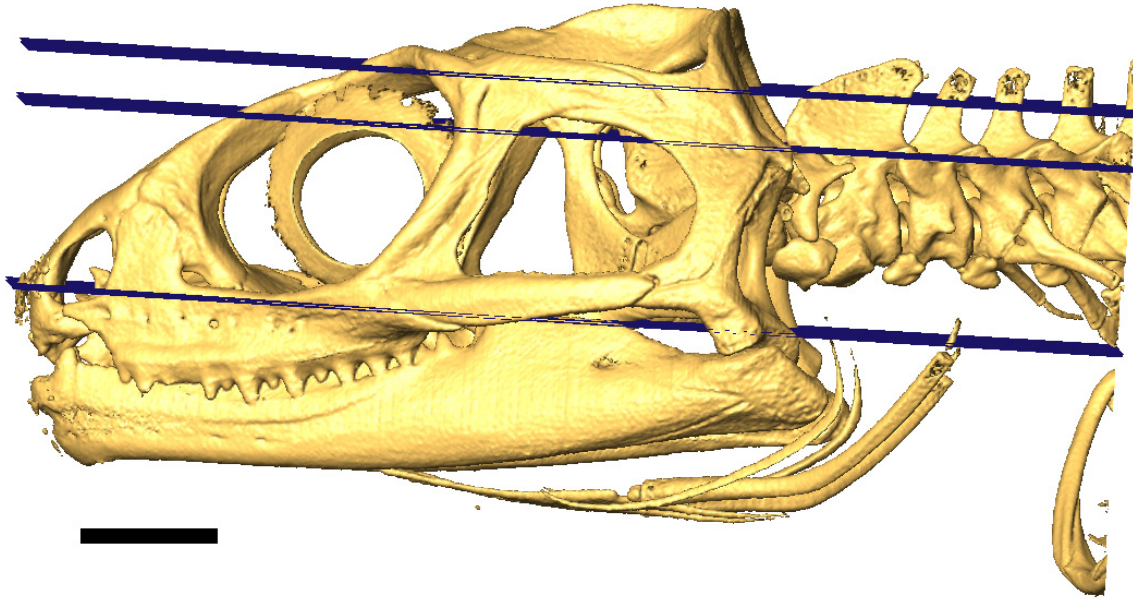


FIGURE 18. Skull model of *Sphenodon* (YPM 9194), based on CT data, in left lateral view demonstrating the location of the schematic horizontal cross-sections shown in Figure 19.

men BMNH 1969.2204 confirms that the mAMES does have a large attachment on the lateral surface of the dentary (Figure 23) but also suggests that no part of it originates from the lower temporal bar. When sectioned, the muscle is quite distinct from the other adductor muscles (Figure 24). This muscle does not leave an obvious shelf on the

dentary bone as found in many squamates and as suggested for sauropterygians (Figure 5) (Rieppel 2002).

m. Adductor Mandibulae Externus Medialis (mAMEM). Lakjer (1926) referred to the m. Adductor Mandibulae Externus Medialis as Part 2. In general terms the mAMEM originates from the

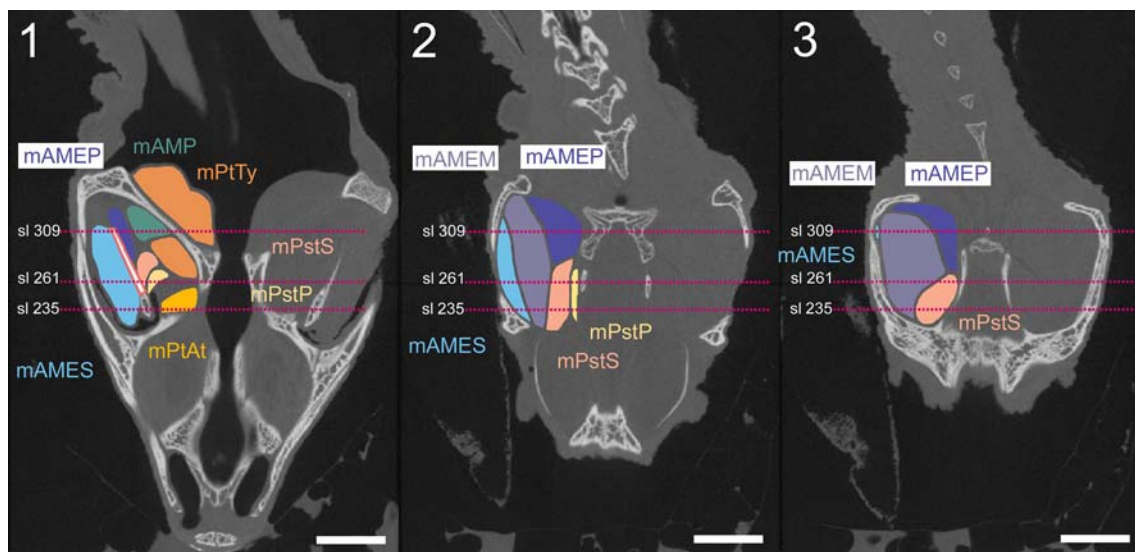


FIGURE 19. Horizontal CT slices with schematic representations of the muscles and basal aponeurosis added. 19.1 Slice 302 through the ventral part of the adductor chamber. 19.2 Slice 184 through the dorsal part of the adductor chamber. Locations of the coronal slices are shown in red. 19.2 Slice 302 through the dorsal part of the adductor chamber. Scale equals 10 mm.

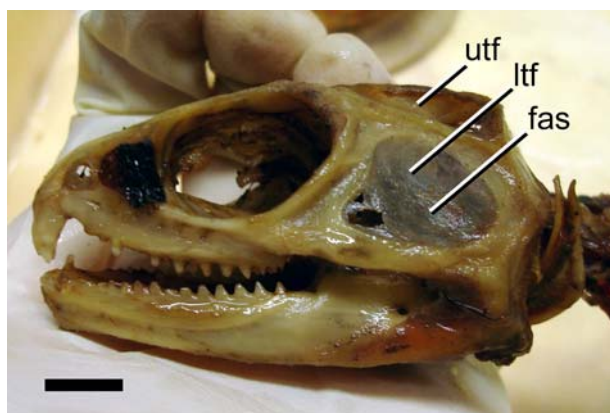


FIGURE 20. *Sphenodon* skull (BMNH1922.6.16.2) in left lateral view showing fascia covering the lower temporal fenestra. Scale equals 10 mm.

posteromedial boundary of the upper temporal fenestra (posterior to the m. Pseudotemporalis Superficialis) (Figures 15, 16, 17, 18, 19, 21, 22, 26, and 27). Abdala and Moro (2003) code the area of origin as simply “parietal and squamosal.” Insertion takes place on the lateral surface of the aponeurosis of the lower jaw (Anderson 1936; Haas 1973; Gorniak et al. 1982; Wu 2003) (Figures 16, 17, 18, 19, 24, and 25).

Details of the insertions seem to differ between individuals. Wu (2003) was unable to distinguish any obvious subdivisions but Gorniak et al. (1982) described three separate portions in the two specimens available to them (Figure 26):

1. The ventrolateral head (mAMEMa) – originates from the posterolateral and posteroventral surfaces of the parietal and from the anterior surface of the dorsal process of the squamosal, inserting into the anterior and central sections of the basal aponeurosis.
2. The anteromedial head (mAMEMb) – originates on the dorsolateral surface of the parietal crest and inserts into the anterodorsal extension of the basal aponeurosis.
3. The posterior head (mAMEMc) – originates from the posterolateral surface of the parietal and the anterodorsal surface of the squamosal, inserting into anterior and central portions of the basal aponeurosis dorsal to the insertion of the ventrolateral head.

Haas (1973) listed five subdivisions but the last two subdivisions are probably included within the m. Adductor Mandibulae Externus Superficialis *sensu stricto* of other authors.

- 1.2a, an anteromedial head (mAMEM2a) – originates from the posteromedial boundary of the upper temporal fenestra (possibly equivalent to mAMEMb of Gorniak et al. 1982).
- 2.2b, a posterior head (mAMEM2b) – originates from the posteromedial boundary of the upper temporal fenestra (possibly equivalent to equivalent to mAMEMc of Gorniak et al. 1982).
- 3.2c, (mAMEM2c) – originates from the squamosal portion of the upper temporal bar (elsewhere treated as part of the mAMES).

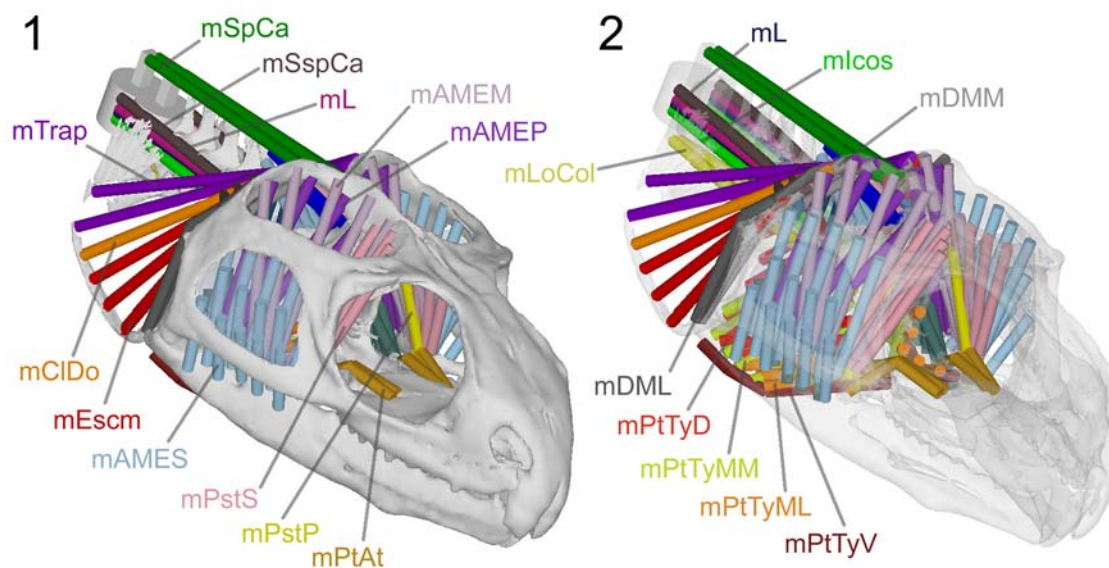


FIGURE 21. Skull model of *Sphenodon* (LDUCZ x036), based on CT data with muscles represented as linear cylinders. 21.1 Anterdorsal view. 21.2 Anterdorsal view with the bone as transparent.

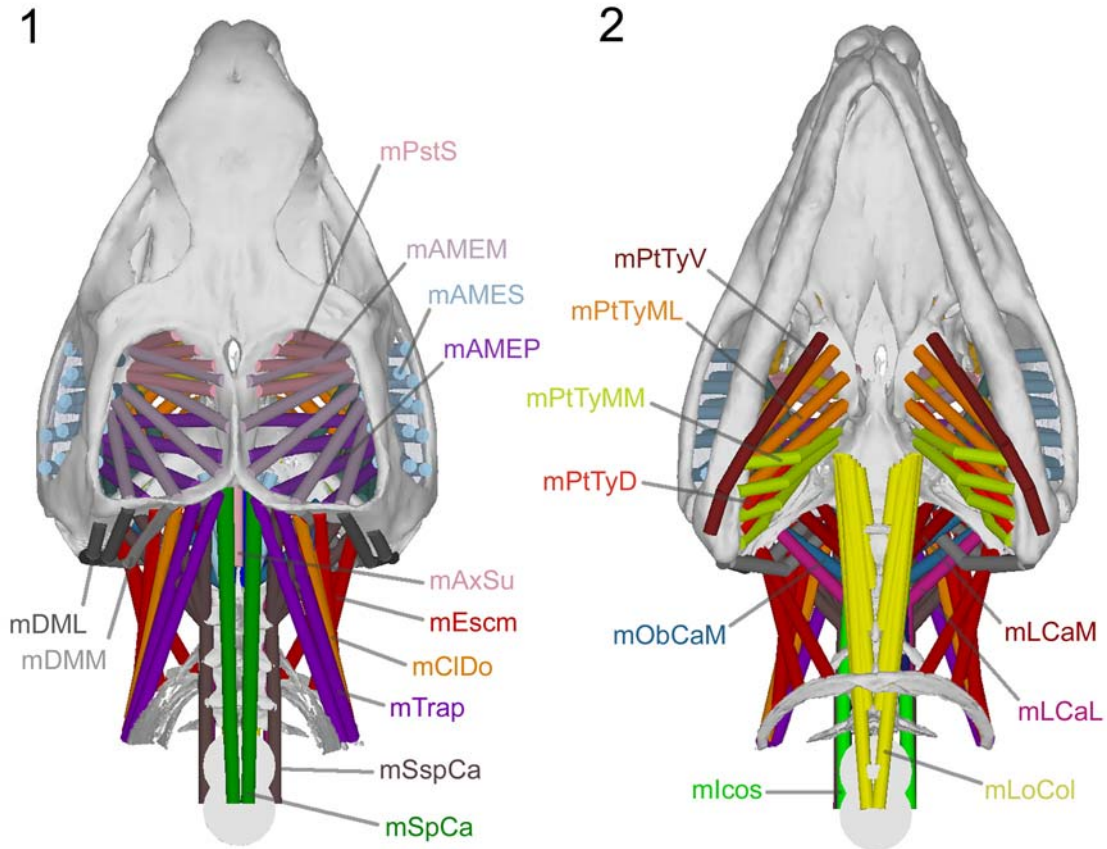


FIGURE 22. Skull model of *Sphenodon* (LDUCZ x036), based on CT data with the muscles represented as linear cylinders. 22.1 Dorsal view. 22.2 Ventral view.

4.2d, (mAMEM2d) – Haas (1973) simply states that it originates from “the upper temporal arch” but see below (elsewhere this head is treated as part of the mAMES [e.g., Poglayen-Neuwall 1953]).

5.2e, (mAMEM2e) – Haas (1973) simply states that it originates from “the upper temporal arch” but see below (elsewhere this head is treated as part of the mAMES [e.g., Poglayen-Neuwall 1953]).

Of the five divisions outlined, Haas (1973) only labelled the first four in his figure 10 (p. 300). Furthermore, as noted by Gorniak et al. (1982, p. 327), the subdivisions that are labelled do not juxtapose to one another as described in the text. Contrary to the figure captions (e.g., Haas 1973, p. 300, figure 10a), we suggest that “MAMEB” does not correspond to 2b but instead to 2a, “MAMEC” refers to 2b rather than 2c; and “MAMEA” refers to 2c and not 2a. The label “MAMED” probably does refer to 2d, but in Haas (1973, p. 300, figure 10b) there appears to be a distinct muscle portion between the parts labelled “MAEMD” and “MAEMA”. This may represent the muscle described as 2e, or alternatively 2d if “MAEMD”

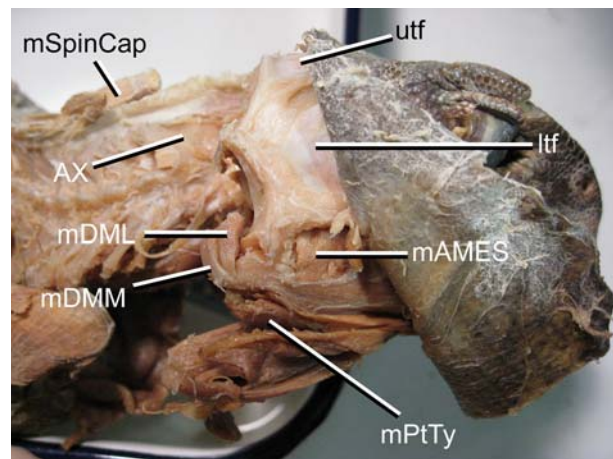


FIGURE 23. *Sphenodon* (BMNH 1969.2204) head and neck in right lateral view showing the m. Adductor Mandibulae Externus Superficialis attaching to the lateral surface of the lower jaw.

represents 2e. This suggests the mAMEMd and mAMEMe of Haas (1973) arise from the squa-

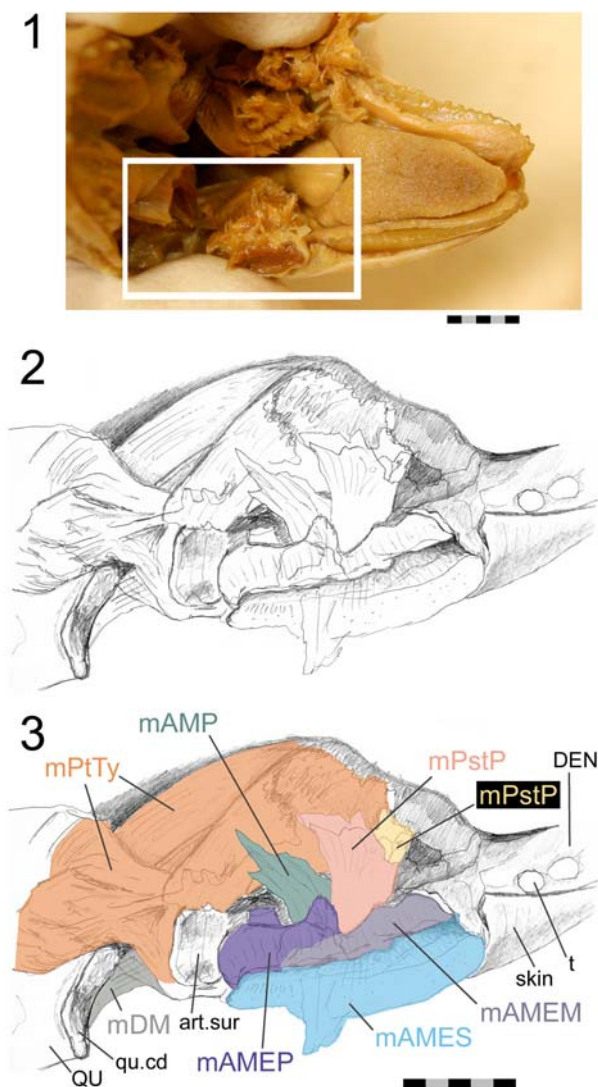


FIGURE 24. *Sphenodon* tongue and adductor chamber (BMNH1972.1223) in dorsal view. 24.1 Close up of the adductor chamber showing a cross-section through the jaw muscles (24.2, 24.3) as indicated by the white box. Note that in 24.2 and 24.3 the anterior part of the articular surface is hidden by the adductor muscles. Scale equals 5 mm.

mosal at the posterior part of the upper temporal bar.

Haas (1973) included divisions 2d and 2e within the m. Adductor Mandibulae Externus Medialis (mAMEM) because they both insert on the lateral surface of the basal aponeurosis, the diagnostic criterion used by Lakjer (1926). However, other authors consider these portions to be part of the m. Adductor Mandibulae Externus Superficialis (e.g., Gorniak et al. 1982; Wu 2003). We follow the latter interpretation. The upper tem-

poral fenestra is covered by a sheet of soft tissue (right side of BMNH 1969.2204, right side of one FMNH 270560 skull) but the muscles do not originate from it.

m. Adductor Mandibulae Externus Profundus (mAMEP). Lakjer (1926) referred to the mAMEP as Part 3. In general, it arises deep to the mAMEM and inserts on the medial surface of the basal aponeurosis posterior to the insertion of the m. Pseudotemporalis Superficialis (mPstS) (Figures 15, 16, 17, 18, 19, 21, 22, 27, and 28) (Haas 1973; Gorniak et al. 1982; Wu 2003). The mAMEP is usually described as having two distinct heads of origin (e.g., Haas 1973; Wu 2003; Gorniak et al. 1982), but there is disagreement as to the positions of their origins, which could mean that they are not actually equivalent.

According to Haas (1973), the two heads include a posteroventral head (3a) originating from the posterodorsal process of the prootic, and a dorsal head (3b) originating from the posterolateral surface of the upper temporal fenestra (anterior surface of the parietal squamosal process and part of the posteromedial surface of the squamosal). By contrast, neither of the portions described by Wu (2003) include the prootic as a site of origin. Instead he lists a main portion with fibres that originate from the posterior wall of the upper temporal fenestra and a posteroventral head that originates from the anterolateral surface of the medial process of the squamosal and the dorsolateral surface of the quadrate, posterolateral to the origin of the m. Adductor Mandibulae Posterior. The situation according to Gorniak et al. (1982) is different again, with both portions, “lateral” and “medial”, described as arising from the prootic, more specifically from its posterolateral and anterolateral surfaces respectively, although the lateral head is figured as if arising from the squamosal (Gorniak et al. 1982, p. 328, figure 2).

Direct examination of BMNH.1969.2204 shows that parts of the m. Adductor Mandibulae Externus Profundus attaches to the posteroventral edge of the posterior temporal bar (parietal and squamosal) and loops anteriorly into the adductor chamber (Figure 28). This perhaps corresponds to the lateral head of Gorniak et al. (1982) and part of the dorsal (3b) head of Haas (1973). The majority of the muscle attaches to the fascia of the posterior temporal bar. There are also fibres visible near the top of the quadrate, which is consistent with the posteroventral part of the m. Adductor Mandibulae Externus Profundus as observed by Wu (2003, p. 591). However, these fibres may instead corre-

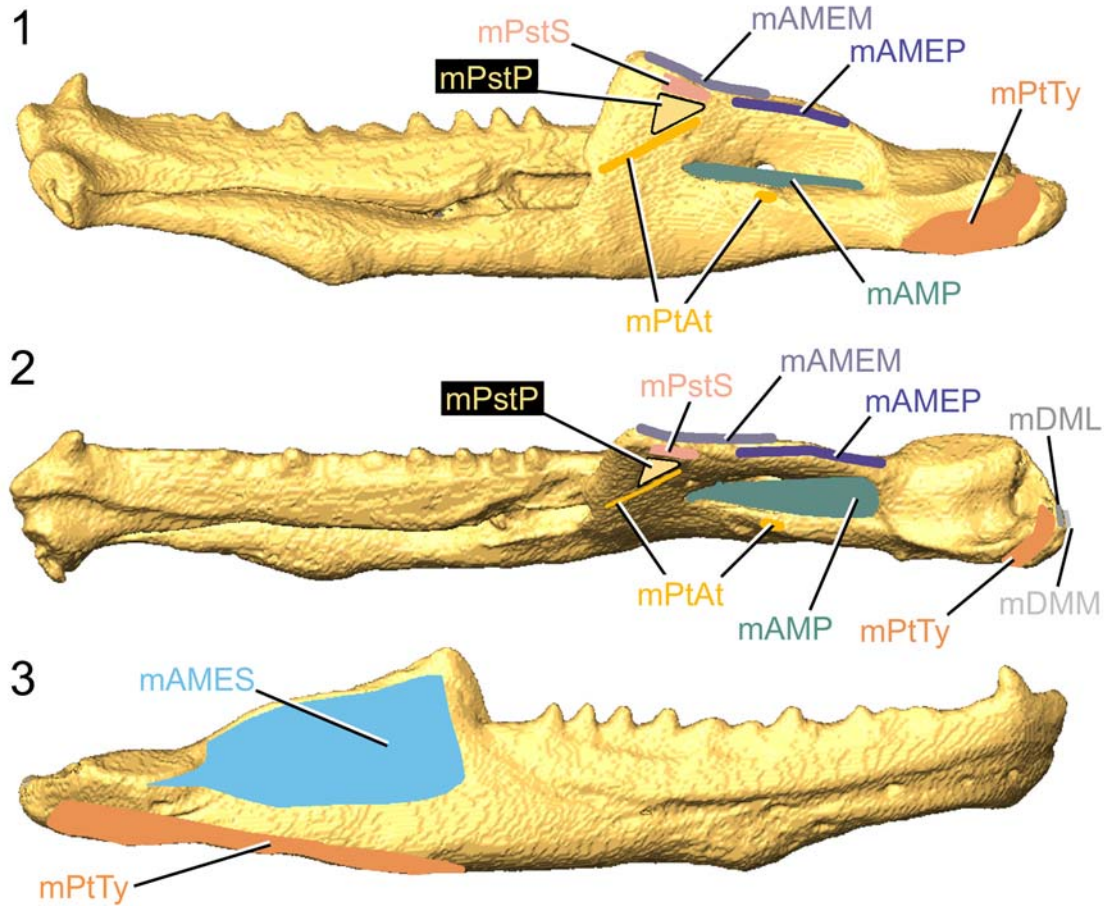


FIGURE 25. Right lower jaw model of *Sphenodon* (LDUCZ x036), based on micro CT data, labelled with areas of muscle attachment according to Haas (1973), Gorniak et al. (1982) and Wu (2003). 25.1 Medial view. 25.2 Dorsomedial view. 25.3 Lateral/labial view. The bump on the ventral surface is a pathology probably acquired from infection of a wound received during fighting with conspecifics.

spond to the m. Protractor Pterygoidei (Ostrom 1962; Haas 1973).

It is difficult to reconcile the differences between descriptions of the m. Adductor Mandibulae Externus Profundus but there is a general consensus that the muscle originates in the posterodorsal corner of the adductor chamber and attaches to the medial surface of the basal aponeurosis (Poglayen-Neuwall 1953; Haas 1973; Gorniak et al. 1982; Wu 2003). Discrepancies found in descriptions and observations may stem from intraspecific variation.

m. Adductor Mandibulae Internus (mAMI)

The m. Adductor Mandibulae Internus comprises the m. Pseudotemporalis and the m. Pterygoideus. These muscles lie between the

ophthalmic nerve (cn5.1) and the maxillary nerve (cn5.2), anteromedial to the m. Adductor Mandibulae Externus.

m. Pseudotemporalis (mPst). The m. Pseudotemporalis seems to correspond, at least in part, to the “pterygoideus externus” of Byerly (1925) who considered this muscle important for closing the mouth, but also for protraction of the lower jaw. Gorniak et al. (1982) demonstrated that the m. Pterygoideus Typicus is more important for the latter role. The m. Pseudotemporalis is usually divided into superficial and deep parts (e.g., Anderson 1936; Gorniak et al. 1982; Barghusen 1973; Holliday and Witmer 2007), although Haas (1973, p. 301) cautions that they are not “sharply separated” from each other.

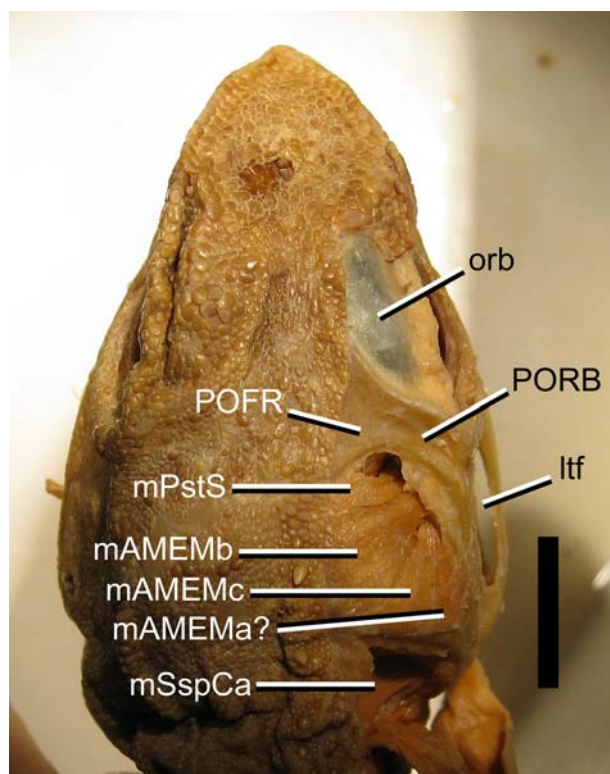


FIGURE 26. Subadult *Sphenodon* head (BMNH1972.1223) in dorsal view with the skin and superficial tissues removed from the right side. Scale equals 10 mm.

The m. Pseudotemporalis Superficialis (mPstS) originates in the anterior third of the upper temporal fenestra (Figures 15,16, 17, 18, 19, 21, 22, 26, and 27): namely the anterolateral surface of the parietal and posterior surface of the postfrontal (Anderson 1936; Haas 1973; Barghusen 1973; BMNH 1972.1223). Wu (2003) also reported that some fibres come from the posterodorsal tip of the epipterygoid. Its posterior fibres are partly overlain by the m. Adductor Mandibulae Externus Medialis (Anderson 1936; Gorniak et al. 1982). Byerly (1925), Anderson (1936) and Gorniak et al. (1982) described the area of origin as extending onto the prootic and the posterolateral edge of the lateral process of the postorbital, but this has not been confirmed or accepted by subsequent workers such as Wu (2003).

The muscle inserts into the medial surface of the basal aponeurosis with some fibres converging on a tendinous extension in a bipennate manner (Anderson 1936; Haas 1973). Wu (2003) also reported that some fibres insert directly into the posteromedial edge of the coronoid process (Figures 24 and 25.1). This may correspond to the point of insertion listed by Byerly (1925) for the

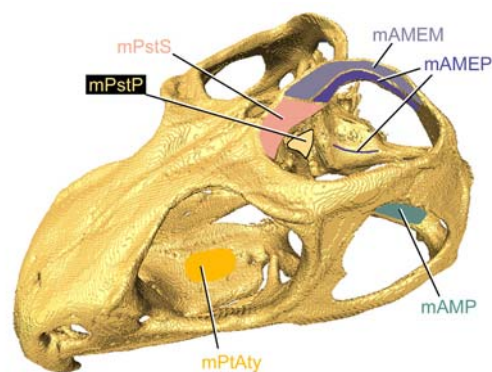


FIGURE 27. Skull model of *Sphenodon* (LDUCZ x036), based on micro CT data, labelled with the areas of muscle attachment.

“pterygoideus externus.” Gorniak et al. (1982) described the insertion in the most detail and referred to three sets of fibres:

1. Anterior fibres. These insert via a tendinous extension to the medial surface of the anterior part of the basal aponeurosis.
2. Central fibres. These insert on the anterior section of the tendinous extension, ventral and posterior to the anterior fibres.
3. Posterior fibres. These attach directly into the medial surface of the anterior and central portions of the basal aponeurosis.

The m. Pseudotemporalis profundus (mPstP) is described by Haas (1973) as “entirely fleshy” and by Wu (2003) as being thin and rectangular (Figure 29). It is closely associated with the m. Adductor Mandibulae Posterior (mAMP) (Lakjer 1926; Haas 1973). Both Haas (1973) and Gorniak et al. (1982) described two parts for this muscle, with one effectively overlying the other:

1. The external layer (long lateral part of Gorniak et al. 1982) originates from the anterolateral edge of the parietal and epipterygoid, and also separately from the posterodorsal expansion of the epipterygoid (Haas 1973; Gorniak et al. 1982).
2. The internal layer (short medial part of Gorniak et al. 1982) originates from the membranous wall of the braincase (Haas 1973). Gorniak et al. (1982) also described some fibres originating from the anterior part of the epipterygoid.

Wu (2003) agreed with previous descriptions but did not subdivide the muscle and reported no contribution from the parietal.

TABLE 2. Muscle weight and fibre lengths data for the jaw muscles of *Sphenodon* according to Gorniak et al. (1982). Note that data for the mAMP do not seem to have been collected.

Muscle		abbrev	Wet weight	Dry weight	Fibre lengths (mm)
m Depressor Mandibulae	lateral	mDM	0.49	0.11	8-21
	medial				23-29
m Adductor Mandibulae Externus Superficialis	anterior	mAMES	0.9	0.35	7-18
	posterior				10-15
m Adductor Mandibulae Medialis	ventrolateral	mAMEMa	0.5	0.1	9-13
	anteromedial	mAMEMb	0.34	0.06	12-17
	posterior	mAMEMc	0.2	0.05	13-15
m Adductor Mandibulae Externus Profundus		mAMEP	0.1	0.04	5-11
m Pseudotemporalis Superficialis		MPstS	0.54	0.12	8-18
m Pseudotemporalis Profundus		mPstP	0.18	0.06	14-17
m Pterygoideus Typicus	dorsal	mPtTyp	0.08	0.02	5-10
	middle		1.65	0.57	17-18
	ventral		0.3	0.08	7-15
m Pterygoideus Atypicus		mPtAty	0.11	0.05	18-20
					16-17

There is general agreement that insertion takes place on the medial surface of the lower jaw on or below the coronoid bone (Figure 24 and 25) (Anderson 1936; Haas 1974; Gorniak et al. 1982; Wu 2003). Haas (1973) described a long area of attachment on the lingual surface of the lower jaw from the anterior end of the coronoid process, along the prearticular edge of the adductor fossa, to the level of the mandibular foramen. This corresponds to the description of Gorniak et al. (1982, p. 330 and figure 2). Wu (2003, p. 592) again records insertion on the medial surface of the coronoid but also to “the anterior part the medial surface of the surangular,” presumably above the adductor fossa.

m. Pterygoideus (mPt). The m. Pterygoideus is composed of two parts; a large fleshy m. Pterygoi-

deus Typicus and a smaller anteriorly placed m. Pterygoideus Atypicus (Anderson 1936; Barghusen 1973; Haas 1973; Gorniak et al. 1982; Wu 2003). The latter is unknown in any extant squamates (Haas 1973; Gomes 1974). In general this muscle group is most important when the gape is large (Byerly 1925; Olson 1961; Jones 2008), but it also plays an important role during protraction of the lower jaw (Gorniak et al. 1982).

The m. Pterygoideus Typicus (mPtTy) is large, complex, and conspicuous, bulging ventrally below the posterior end of the lower jaw (Figures 14, 16, 17, 18, 19, 22.2, and 23; Byerly 1925; Haas 1973; Gorniak et al. 1982; Wu 2003; FMNH270560, BMNH1969.2204). According to Gorniak et al. (1982) it is the heaviest muscle in the skull (Table

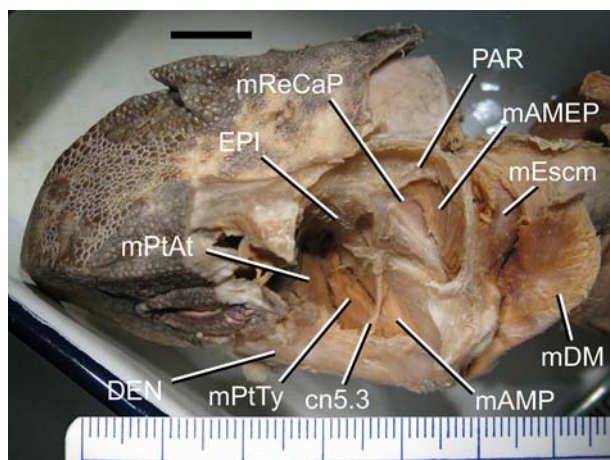


FIGURE 28. *Sphenodon* (BMNH 1969.2204) head in dorsolateral view with some muscles still attached. Scale equals 10 mm.

2). Elsewhere, this muscle is referred to as the “pterygoideus ventralis” (e.g., Holliday and Witmer 2007), “pterygoideus posterior” (e.g., Schumacher 1973b; Busbey 1989), or the “pterygoideus internus” (Byerly 1925). Gorniak et al. (1982) provided the most detailed account of this muscle in *Sphenodon* and considered it in three parts:

1. A dorsal (or deep) (mPtTyD) part that originates from the medial surface of the pterygoid

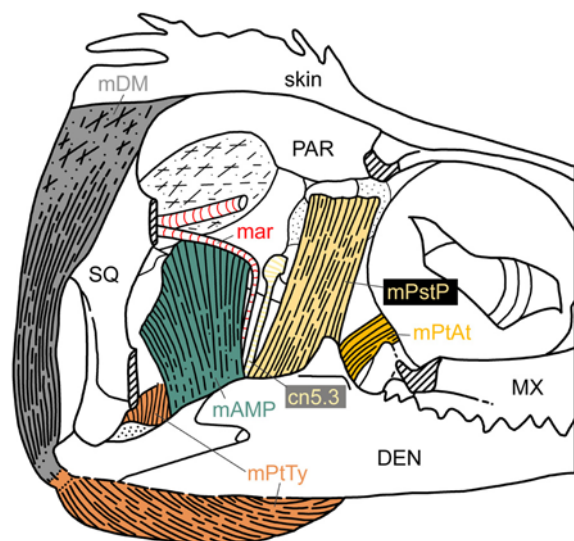


FIGURE 29. The adductor chamber in *Sphenodon* in left lateral view showing the m. Adductor Mandibulae Posterior and the m. Pseudotemporalis Profundus (the postorbital bar, lower temporal bar, upper temporal bar, m. Adductor Mandibulae Externus and m. Pseudotemporalis Profundus have all been removed). Redrawn from Wu (2003).

along its anterodorsal margin (Figures 30, 31 and 32). It inserts into the dorsomedial surface of the posterior end of the lower jaw (on the dentary) by way of fine tendons and fleshy attachment (Figures 22, 25.1 and 30).

2. A middle part (the largest part) (mPtTy: mPtTyML and mPtTyML) that originates on the ventral and medial surfaces of the ectopterygoid-ptyergoid process, the medial margin and posteroventral half of the pterygoid, and the anteromedial process of the quadrate (Figures 30, 31 and 32). The anterior limit of origin is marked by the “medial pterygoid crest,” which is visible in a ventral view of a dried skull (Barghusen 1973; Gorniak et al. 1982) (Figures 3.1, 14, and 22). It inserts on the posteromedial surface of the lower jaw on the dentary, just anterior to the insertion of the dorsal portion (of the mPtTy) (Figures 22, 25, and 30).
3. A ventrolateral part (mPtTyV) that originates via a tendon from the lateral and ventral surfaces of the ectopterygoid-ptyergoid process (Figures 30 and 32) and inserts on the medial, ventral, and ventrolateral surfaces of the posterior third of the dentary (Figures 22, 25 and 30).

The relationship between the posterolateral surface of the quadrate-ptyergoid wing and the mPtTy (middle part) is unclear. Consistent with Gorniak et al. (1982), several authors (e.g., Barghusen 1973; Haas 1973; Wu 2003) describe and figure the m. Pterygoideus Typicus (middle part) as originating on the ventrolateral part of the quadrate. However, in specimen BMNH 1969.2204, some of the muscle previously considered part of the m. Pterygoideus Typicus (e.g., Figure 31, Wu 2003, figure 8) can be seen to lie posterior to the mandibular division of the trigeminal nerve and a boundary of transparent connective tissue (Figures 28 and 33). Therefore, this portion of muscle strictly represents a portion of m. Adductor Mandibular Posterior (Figure 32). It also appears to insert into the mandibular fossa rather than more ventrally.

The relationship between the posteromedial surface of the quadrate-ptyergoid wing and the middle part of the m. Pterygoideus Typicus is also unclear. Examination of BMNH 1969.2204 suggests that only the ventral edge provides a site of origin (Figure 34), whereas one of the skulls registered as FMNH 270560 and CT data of specimen YPM 9194 suggest—that fibres originate from the entire anteroventral corner (Figures 17.3 and 19.1).

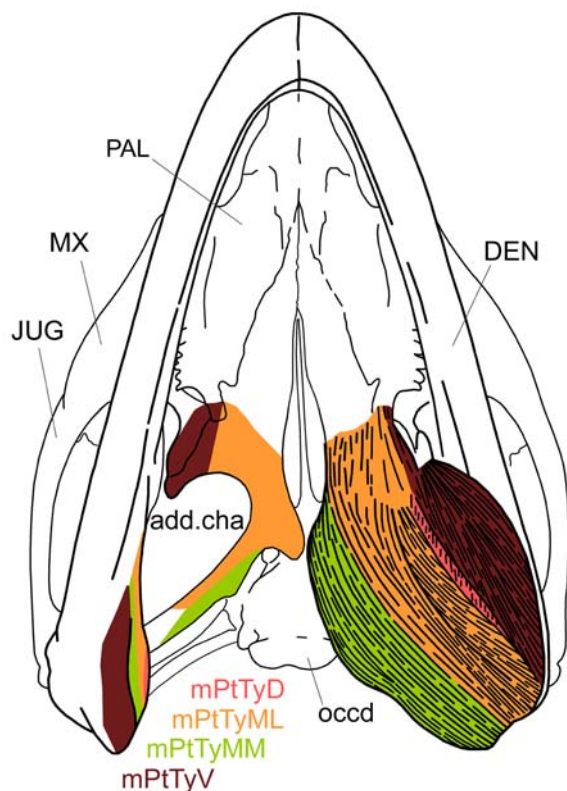


FIGURE 30. Detail of the m. Pterygoideus Typicus of *Sphenodon* in ventral view. Redrawn from Gorniak et al. (1982).

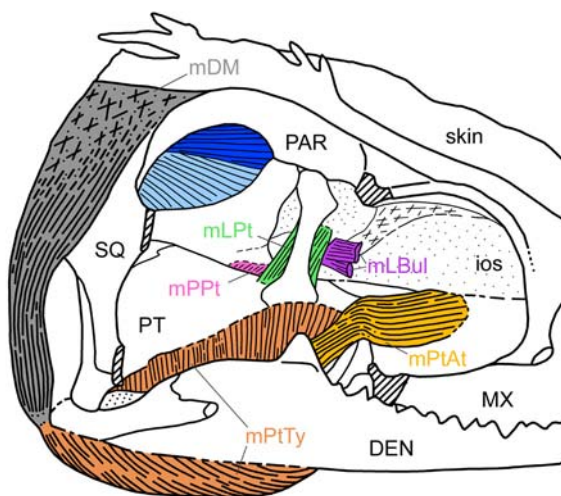


FIGURE 31. The adductor chamber in *Sphenodon* in left lateral view showing the m. Pterygoideus Atypicus and m. Constrictor Internus Dorsalis group (the postorbital bar, lower temporal bar, upper temporal bar, pseudotemporalis and all adductor mandibulae have been removed). Redrawn from Wu (2003).

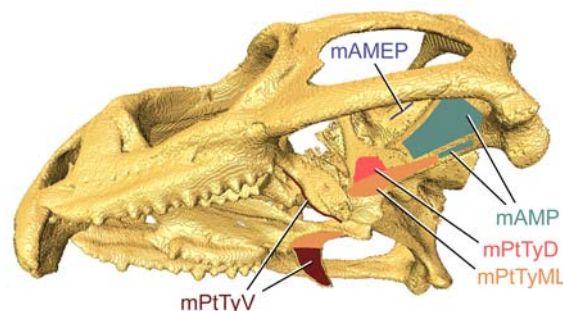


FIGURE 32. Skull model of *Sphenodon* (LDUCZ x036), based on CT data, in ventrolateral view labelled with the areas of muscle attachment.

Specimens BMNH 1969.2204 and BMNH 1972.1223 show an additional, previously unreported, insertion for posterior fibres of the m. Pterygoideus Typicus onto the dorsal surface of the lower jaw in a depression behind the articular surface and in front of the m. Depressor Mandibulae (Figure 35). Near this location in specimen PCDG2 there is a tubercle that might be associated with the attachment of muscle fibres (Figure 36). This aspect of the m. Pterygoideus Typicus seems previously to have been overlooked and would probably add stability (via an opposing force) during protrusions of the lower jaw. When activated the majority of the m. Pterygoideus Typicus will aid in closing the jaw, but the action of these posterior-most fibres will provide an opposite, opening force.

The m. Pterygoideus Atypicus (mPtAt) is probably equivalent to the pterygoideus anterior, dorsalis, or lateralis in archosaurs (Witmer 1987; Holliday and Witmer 2007). It is not found in squamates (Haas 1973; Wu 2003), and in *Sphenodon* it is quite small compared to the m. Pterygoideus Typicus, being less than 10% the weight (e.g., Gorniak et al. 1982; Wu 2003). Correspondingly it seems to have been overlooked by some workers (e.g., Byerly 1925). Nevertheless, the path of this muscle is very different from any other muscle in the skull and probably plays an important role in jaw movement (Gorniak et al. 1982).

The m. Pterygoideus Atypicus originates via a tendon from the dorsal surface of the palate (below the eye) close to, or on, the palatine-pterygoid joint (Haas 1973; Gorniak et al. 1982; Wu 2003) (Figure 16, 17, 18, 19, 21, 27, 31, and 37). The area of origin may also include the base of the interorbital septum (Haas 1973; Wu 2003). Posteriorly it extends and loops over the dorsal surface of the pterygoid flange (Figure 21, 31) (e.g. BMNH 1969.2204; Haas 1973; Gorniak et al. 1982; Wu

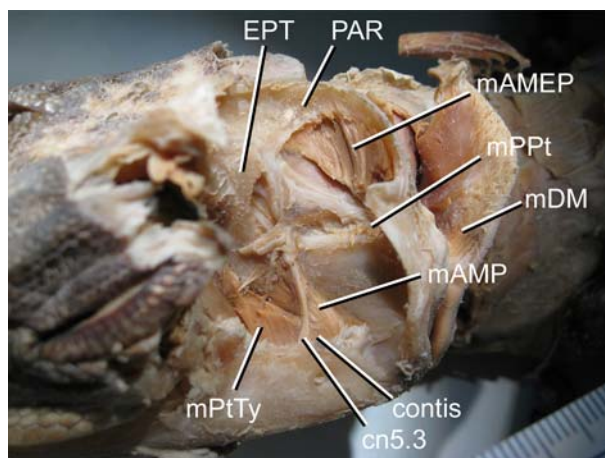


FIGURE 33. *Sphenodon* (BMNH 1969.2204) head in anterolateral view with both the upper and lower temporal bars removed showing parts of the m. Pterygoideus Typicus, m. Adductor Mandibulae Externus Profundus and m. Protractor Pterygoidei.

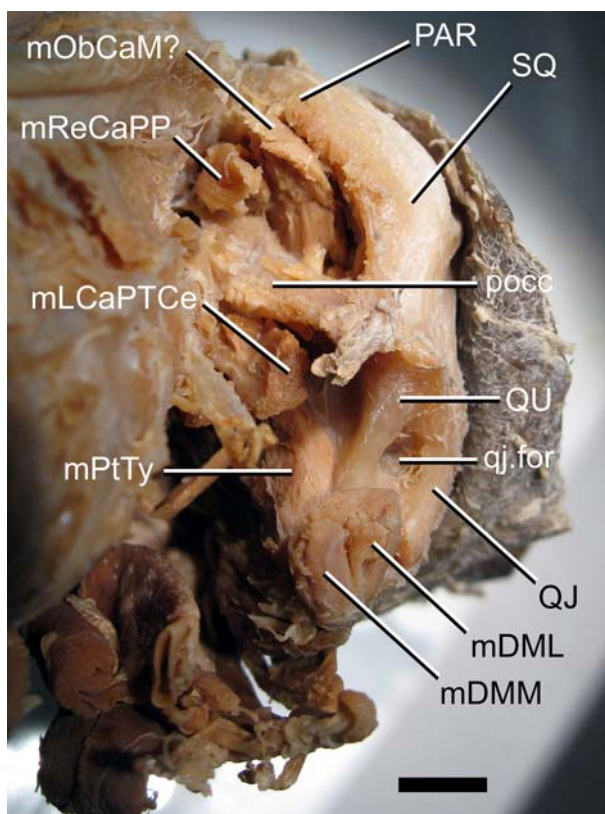


FIGURE 34. Right side of a *Sphenodon* head (BMNH 1969.2204) in posterior view showing the anterior heads of the m. Depressor Mandibulae, m. Rectus Capitis Posterior Profundus, m. Longissimus Capitis Pars Transversalis Cervicis.

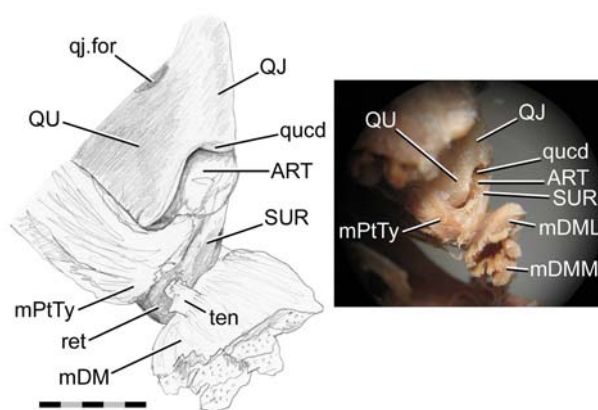


FIGURE 35. Posterior end of a *Sphenodon* lower jaw (BMNH 1969.2204) in posterodorsal view showing a portion of the m. Pterygoideus Typicus that inserts onto the lower jaw posterior to the jaw joint. Scale equals 5 mm.

2003) as it does in both crocodiles and turtles (Schumacher 1973b; Holliday and Witmer 2007).

The muscle attaches to the lower jaw on or near the coronoid bone, but the exact location appears subject to individual variation. Haas (1973) observed it to insert below the coronoid, Poglayen-Neuwall (1953) described it as inserting into the anterior edge of the coronoid, and Gorniak et al. (1982) described it attaching ventral and posterior to the coronoid (Figure 25.1). Wu (2003) reported two distinct tendinous insertions of this muscle, and in his account the main part (~80%) of the muscle mass was said to insert onto the posteroventral margin of the coronoid (just above and in front of the adductor fossa), whereas the remaining 20% inserts onto the lower margin of the adductor fossa (Wu 2003, figure 17A) (Figure 25.1).

m. Adductor Mandibulae Posterior (mAMP)

This muscle originates from the quadratus and inserts within the adductor fossa of the lower jaw (Haas 1973; Wu 2003; Holliday and Witmer 2007). When the jaws are closed the fibres are orientated so that they are nearly vertical (Haas 1973; Wu 2003).

This muscle was not specifically described by Gorniak et al. (1982), but Wu (2003, p. 595) suggested it was figured as part of the m. Adductor Mandibulae Externus Profundus (Gorniak et al. 1982, figure 1) because a portion is clearly visible posterior to the course of the mandibular division of the trigeminal nerve (cn5.3). Perhaps significantly, both Lakjer (1926) and Haas (1973) noted that the m. Adductor Mandibulae Posterior (mAMP) and m. Adductor Mandibulae Profundus

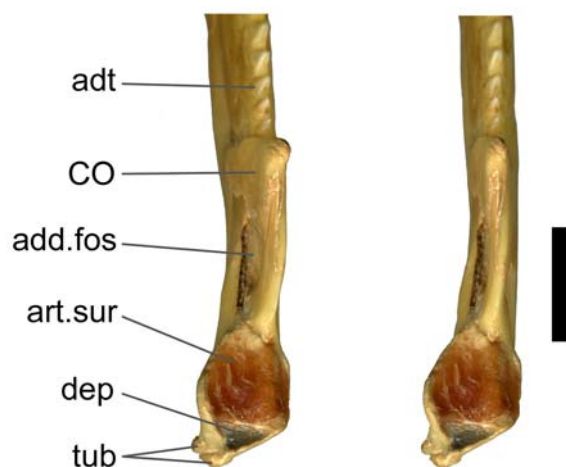


FIGURE 36. Stereopair showing the posterior end of a *Sphenodon* lower jaw (DGPC2) in dorsal view. Scale equals 10 mm.

(mAMEP) can appear to be poorly separated. However, in the same figure by Gorniak et al. (1982) this portion of muscle is drawn as if it attaches to the crest of the lower jaw rather than the adductor fossa, as would be expected according to Haas (1973) and Wu (2003). As Gorniak et al. (1982, figure 1) reported no muscle originating from the quadrate, as would be expected for the mAMP, the muscle may have been absent in the specimens examined or was overlooked entirely. Abdala and Moro (2003) coded the mAMP as present in *Sphenodon*. Barghusen (1973) figured a large area of origin for the mAMP on most of the lateral surface of the pterygoid process of the quadrate (Figures 16, 17.3, 29, and 32). In specimen BMNH 1969.2204 this region is largely free of muscle but this could be because some or all of the muscle was removed during previous dissection (e.g., Figures 28 and 33).

A group of muscle fibres runs from the ventral part of the pterygoid process of the quadrate towards the adductor fossa. This has been considered part of the m. Pterygoideus Typicus in previous descriptions (e.g., Figure 29, 31; Wu 2003, figure 8). Nonetheless, in specimen BMNH 1969.2204 it is clearly situated posterior to the mandibular division of the trigeminal nerve (Figure 28) and is separated from the m. Pterygoideus Typicus by a portion of transparent connective tissue (Figure 33); it therefore probably represents part of the mAMP (Figure 32). A bundle of muscle fibres attached to the adductor fossa in BMNH 1972.1223 seems to be the insertion of the mAMP

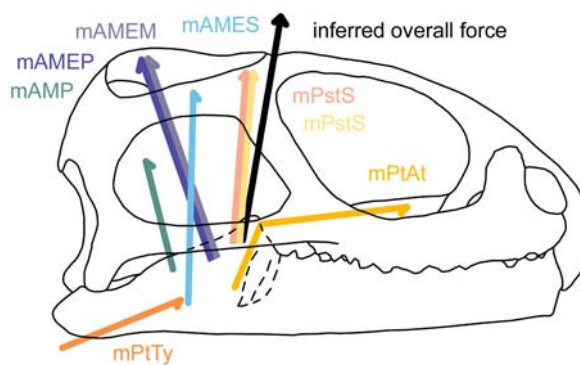


FIGURE 37. The approximate directions of forces generated by jaw muscles during biting in *Sphenodon* according to Wu (2003).

as described previously (Haas 1973; Wu 2003; Holliday and Witmer 2007).

m. Constrictor Internus Dorsalis (mCID)

This muscle group runs between the braincase and the bones that contribute to the palate. It is divided into three parts: the m. Levator Pterygoidei, the m. Protractor Pterygoidei and the m. Levator Bulbi (Figure 31). In general these muscles connect the braincase to the palate (Haas 1973), but do show individual variation (Table 3; Ostrom 1962; Haas 1973; Wu 2003). Byerly (1925) did not describe these muscles.

m. Levator Pterygoidei (mLPt). The m. Levator Pterygoidei lies medial to the ophthalmic nerve (cn5.1) (Holliday and Witmer 2007) and has been described as a thin strip of long fibres (Ostrom 1962). It originates on the “ventrolateral surface of the cartilaginous orbitosphenoid medial to the dorsal extremity of the epipterygoid” (Ostrom 1962, p. 733), and inserts on the medial surface of the epipterygoid base and the dorsal and medial surfaces of the pterygoid (Ostrom 1962) (Figure 38). Poglayen-Neuwall (1953), Haas (1973) and Wu (2003) described similar arrangements but with slight differences in fibre length or extent. Wu (2003) also reported a tendon located posterior and parallel to the m. Levator Pterygoidei (Figure 31). Lakjer (1926), and correspondingly Anderson (1936), did not consider this muscle present in *Sphenodon* but, as Haas (1973) points out, it does seem to have been figured by Lakjer (1926) (Table 3).

m. Protractor Pterygoidei (mPPt). The m. Protractor Pterygoidei is located lateral to the ophthalmic nerve (cn5.1) in lepidosaurs (Holliday and Witmer 2007) and is generally described as a

TABLE 3. Variation in reports regarding the presence absence and extent of the M. Protractor Pterygoidei and m. Levator Pterygoidei.

Reference	m. Protractor Pterygoidei	m. Levator Pterygoidei
Günther (1867)	not mentioned	not mentioned
Osawa (1898)	not mentioned	not mentioned
Edgeworth (1907, 1931, 1935)	referred to as the ? . spheno-pterygo-quadratus? Reported as present in juveniles and usually retained in the adult	not mentioned
Versluys (1910, 1912)	present in juveniles and usually retained in the adult	not mentioned
Adams (1919)	absent	not mentioned
Byerly (1925)	not mentioned	not mentioned
Lakjer (1926)	well developed	reported as absent but seems to have been figured
Lubosch (1933)	not mentioned	present (but referred to as the "M. levator bulbi ventralis")
Poglayen-Neuwall (1953)	absent	present
Ostrom (1962)	considered present ?nd functional?in one specimen but absent in another	present in both specimens examined
Haas (1973)	"present in one specimen, absent in another"	present in both specimens examined
Wu (2003)	present but small	present
Peter Johnson personal communication 2008	present (on both sides of all 4 specimens examined)	not mentioned

broad sheet-like muscle (Anderson 1936; Ostrom 1962; Haas 1973). It originates from the lateral surface of the braincase (dorsal surface of the basisphenoid basipterygoid process, the anteroventral part of the prootic, and the ventral part of the orbitosphenoid) and inserts along the dorsal surface of the quadrate-pterygoid wing (Anderson 1936; Ostrom 1962; Haas 1973). The coronal section drawn by Edgeworth (1907, figure 28) suggests that some anterior fibres of the m. Protractor Pterygoidei ("M. spheno-pterygo-quadratus") may also insert on part of the epipterygoid. Both Ostrom (1962) and Haas (1973) found this muscle to be present in one specimen but absent, or almost absent, in another (Table 3). Wu (2003) also found the muscle in at least one specimen (Figure 31) and although its posterior extent was more limited

than described by Ostrom (1962) (Figure 38), Wu (2003) did report some anterior fibres originating from a tendon next to the m. Levator Pterygoidei. Vestiges of the m. Protractor Pterygoidei may be visible along the dorsal edge of the quadrate in specimen BMNH 1969.2204 (Figure 33).

The m. Protractor Pterygoidei is associated with kinesis in squamates (e.g., Haas 1973). As a result, some authors considered that the presence of this muscle in *Sphenodon* might indicate the potential for some form of kinetic movement (Lakjer 1926; Anderson 1936). However, kinesis has never been recorded in *Sphenodon*, and its sutures do not appear to allow substantial movement between the skull bones (e.g., Haas 1973; Jones 2006a, 2007). Edgeworth (1935) described this muscle as being present in the embryo and

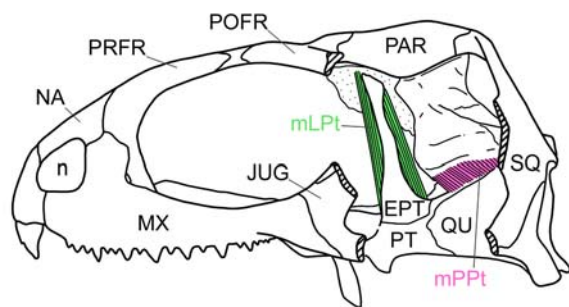


FIGURE 38. *Sphenodon* skull in left lateral view with part of the left temporal region removed showing the location of the m. Protractor Pterygoidei and m. Levator Pterygoidei. Redrawn from Ostrom 1962.

usually retained in the adult leading to suggestions that variation in its development might be related to diet (Ostrom 1962) or ontogeny (Haas 1973). More recent work suggests this muscle is invariably present in adult *Sphenodon* but can easily be overlooked (Peter Johnson pers. comm. 2009).

m. Levator Bulbi (mLBul). The m. Levator Bulbi is the most developed of the three Constrictor Internus Dorsalis muscles (Haas 1973) and is supposedly the least variable (Wu 2003). The m. Levator Bulbi was not described directly by Ostrom (1962), Gorniak et al. (1982), or Wu (2003). Haas (1973) divided it into a dorsal and smaller ventral portion.

The m. Levator Bulbi Ventralis (mLBulV) was found in only one of the two specimens examined by Haas (1973). There it originated from the anterior edge of the membranous wall of the braincase and inserted on the palatal membrane in front of, and distinct from, the m. Levator Pterygoidei (Figure 31).

The m. Levator Bulbi Dorsalis (mLBulD) has a tendinous origin from the anteromedial border of the epipterygoid anterior to the m. Levator Bulbi Ventralis, not from the membranous wall of the braincase (*contra* Lakjer 1926; Poglayen-Neuwall 1953). From there it loops anteroventrally and anterodorsally before inserting on the lower eyelid (Haas 1973). In some individuals its midpoint (ventralpoint) may consist of an internal tendon ("Zwischensehne" Poglayen-Neuwall 1953; Haas 1973, figure 3). An anterior portion may also arise from the pterygoid or palatine joining the main body of the muscle at the point of the tendon (Haas 1973).

m. Constrictor Ventralis Trigemini (mCVT)

This muscle group was used by Haas (1973) to accommodate the anterior part of the m. Intermandibularis since its lateral edge is innervated by

the trigeminal nerve (cn5.3) via the mylohyoid nerve (e.g., Byerly 1925; Poglayen-Neuwall 1953; Rieppel 1978). Problematically the posterior and medial part of the muscle is innervated by the facial nerve (cn7) but unlike squamates, it is not possible to recognize an anterior and posterior division of the muscle by gross anatomy (Rieppel 1978).

m. Intermandibularis (mlnm). The m. Intermandibularis is comprised of transverse fibres that link the anterior three fifths of the lower jaws to one another and wrap around the anterior part of the m. Pterygoid Typicus (Haas 1973; Rieppel 1978). According to Rieppel (1978, p. 431) this muscle "grades" into the m. Constrictor Colli posteriorly (Figure 39). Rieppel's opinion corresponds with the description of Ruge (1896) but not Versluys (1898), von Wettstein (1931, 1932), Poglayen-Neuwall (1953), or Haas (1973). This discord may be another example of intraspecific variation or personal perception. The two muscles are certainly separate in prehatchlings at stage P (Edgeworth 1935, figure 459).

In *Sphenodon* this muscle may assist in guiding the lower jaws during prooral movement. It is clear from the structure of the jaw joint that in order for the lower jaws to move forwards and backwards, the angle between their long axes must change at the symphysis. Although Gorniak et al. (1982) did not observe such relative movements, a ligamentous symphyseal component may allow it to occur (Günther 1867, p. 600; Robinson 1976, p. 54).

OTHER MUSCLES OF THE HEAD

This section describes the remaining muscles of the head that are not innervated by the trigeminal nerve (cn5). Most of these muscles are instead innervated by the facial (cn7), glossopharyngeal (cn9), or hypoglossal (cn12) nerves. They include the superficial muscles of the neck and throat in addition to the depressor mandibulae. In general, these muscles have received less attention than those innervated by the trigeminal nerve.

Aspects of the throat musculature have been described repeatedly (Ruge 1897; Osawa 1898; Edgeworth 1907, 1935; Byerly 1925; von Wettstein 1931, 1932; Lubosch 1933; Lightroller 1939; Haas 1973; Gorniak et al. 1982; Al-Hassawi 2004, 2007), but most notably by Rieppel (1978) who dissected two specimens. Schwenk (1986) also described some of the throat musculature within a detailed description of the tongue, based on histological sections taken from one adult specimen. This largely agreed with the findings and homologies of

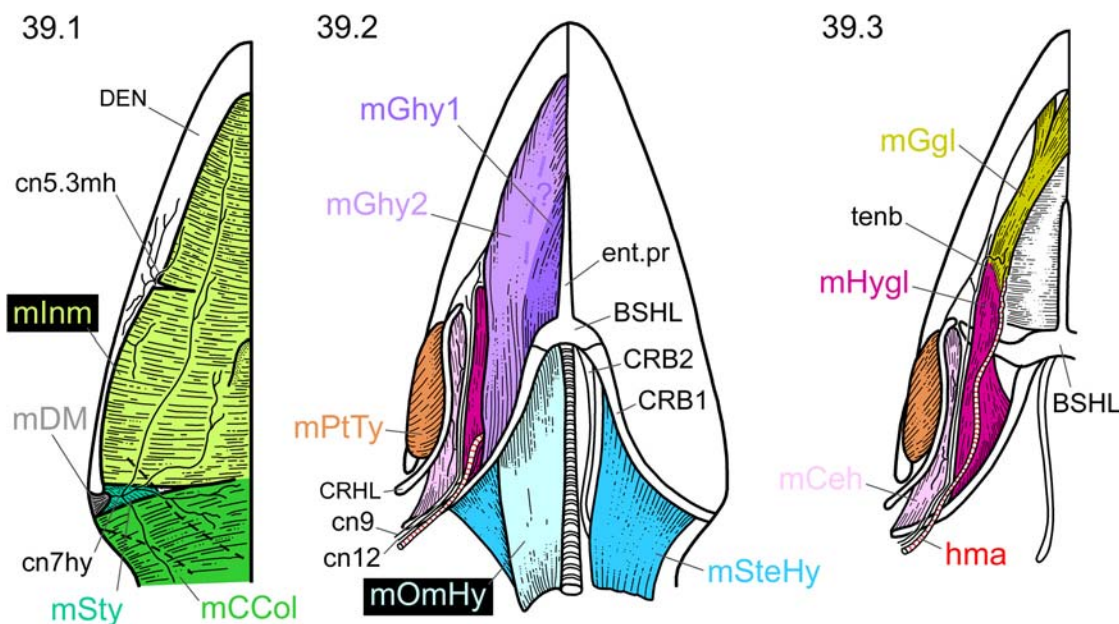


FIGURE 39. Muscles of the throat in *Sphenodon* in ventral view. 38.1 Superficial muscles. 38.2 Deeper muscles. 38.3 Deeper muscles with further dissection medially. Redrawn from Rieppel (1978).

Rieppel (1978) but also contributes new information.

m. Depressor Mandibulae (mDM)

The m. Depressor Mandibulae is perhaps the most noteworthy of the muscles innervated by the facial nerve (cn7) because of its obvious function in controlling jaw opening (Gorniak et al. 1982). Günther (1867) considered this muscle to be integral to the shearing jaw movement, but this was not supported by the detailed findings of Gorniak et al. (1982). Despite its prominence in *Sphenodon*, descriptive accounts of the m. Depressor Mandibulae are often brief (e.g., Osawa 1898; Ruge 1896; Lubosch 1933; Edgeworth 1935; Anderson 1936; Haas 1973) or absent (e.g., Lightroller 1939; Wu 2003), although more detailed descriptions are provided by Byerly (1925), Gorniak et al. (1982), and Al-Hassawi (2004, 2007). Throckmorton (1978) found that the muscle remained active in the squamate *Uromastix* after the jaws had started to close, perhaps to control the position of the quadrate during static biting (Herrel et al. 1998), to modify bite force, or control the speed of jaw closure. No evidence of similar activity was found in *Sphenodon* (Gorniak et al. 1982).

The m. Depressor Mandibulae originates from the posterodorsal edge of the parietal and squamosal, and from a small mid-line portion of connec-

tive tissue (Figures 21, 22, 28, 29, 31, and 33) (Byerly 1925; Gorniak et al. 1982; Al-Hassawi 2004, 2007). Gorniak et al. (1982) described the dorsal third as being thin, the middle third as being thick, and the ventral third as tapering towards the attachment on the lower jaw (Figures 21, 22, 23, 25, 29, 31, 34, and 35). This is confirmed by examination of specimens BMNH 1969.2204 and BMNH 1972.1.22.3. Specimen BMNH 1969.2204 shows that most of the origin is from the squamosal, with the area of origin decreasing medially. Al-Hassawi (2004, 2007) reported the presence of ridges and pits on the bony sites of origin but did not cite a specific specimen. Examination of *Sphenodon* skeletal material does not fully confirm this observation (e.g., LDUCZ x036, LDUCZ x1176). The left squamosal of LDUCZ x036 is roughened along its dorsal edge but the right squamosal is not.

Both Edgeworth (1935) and Haas (1973) described the m. Depressor Mandibulae as undivided, and Abdala and Moro (2003) coded it as such in their cladistic analysis but others have reported that there is evidence of subdivision (e.g., Gorniak et al. 1982; Al-Hassawi 2004, 2007; specimens BMNH 1969.2204, and BMNH 1972.1.22.3). The muscle consists of a thin portion with a more medial origin, m. Depressor Mandibulae Medialis (mDMM, posterior of Gorniak et al. [1982] and externus of Al-Hassawi [2004, 2007]) and a

larger fleshy portion with a more lateral origin, m. Depressor Mandibulae Lateralis (mDML, anterior of Gorniak et al. [1982]; internus of Al-Hassawi [2004, 2007]). There is no obvious connective tissue division (Gorniak et al. 1982) but there are certainly differences in texture and colour. Previous authors have described the division being most obvious at the point of insertion on the lower jaw (Gorniak et al. 1982; Al-Hassawi 2004, 2007). Fibres from the m. Depressor Mandibulae Medialis may be up to three times longer than those of the m. Depressor Mandibulae Lateralis (Table 2) (Gorniak et al. 1982).

According to Gorniak et al. (1982), the fibres from the m. Depressor Mandibulae Medialis curve around the end of the lower jaw and insert on its ventral surface after curving around the fibres of the m. Depressor Mandibulae Lateralis, which attach to the posterolateral end of the lower jaw. In both cases the more superficial the fibres, the further forward on the lower jaw they attach (Gorniak et al. 1982). Al-Hassawi (2004, 2007) also describes a double insertion but one that is more localised and restricted to the posterodorsal end of the lower jaw. Examination of specimen BMNH 1969.2204 and BMNH 1972.1223 corresponds more closely to the description of Al-Hassawi (2004, 2007), and demonstrates that the fibres of both portions converge into a short tendon, which inserts onto a very small area on the posterolateral tip of the lower jaw (retroarticular process) (Figure 35).

Al-Hassawi (2004, 2007) suggested that a depression on the dorsal surface of the retroarticular process was related to the insertion of the m. Depressor Mandibulae, but here we describe this as an attachment point for the middle part of the m. Pterygoideus Typicus. In some individuals a bony tubercle is present near this position (DGPC2, Figure 36), but again this is perhaps more likely to be associated with the m. Pterygoideus Typicus.

Al-Hassawi (2004, 2007) describes a muscle, referred to as the “Cervicomandibularis (Cm),” originating from the dorsal crest of fatty tissue and muscle fascia, overlapping the neural spines of the atlas and axis, and inserting on the retroarticular process. As labelled in her illustration (2004, p. 116; 2007, p. 116) it suggests this represents a posterior portion of m. Depressor Mandibulae (e.g. see Haas 1973).

m. Constrictor Colli (mCCol)

The m. Constrictor Colli (“m. Sphincter Colli” in Poglayen-Neuwall 1953 and Haas 1973) runs

around the anterior and mid-neck regions (Figure 39) and attaches to the muscle fascia of the posterior portions of the m. Depressor Mandibulae (Versluys 1898; Fürbringer 1900; Lubosch 1933; Poglayen-Neuwall 1953; Haas 1973; Al-Hassawi 2004, 2007). Anteriorly this muscle in adults is continuous with the m. Intermandibularis (Rieppel 1978). The anterior portion of the m. Constrictor Colli described by Lubosch (1933) is therefore probably the posterior part of the m. Intermandibularis although this is questioned by Haas (1973) because, as drawn by Lubosch (1933), it is too superficial. It is innervated by the facial nerve (cn7) (Haas 1973).

m. Verbindungsbündel (mVer)

This strip of muscle connects the posterior portion of m. Depressor Mandibulae to the anteroventral part of the m. Constrictor Colli. Correspondingly it is innervated by the facial nerve (cn7). It was reported by both Lubosch (1933, p. 599) and Haas (1973) and also appears to have been figured by Lightroller (1939, figure 19).

m. Intermandibularis (mInm)

This muscle is innervated by both the trigeminal nerve (cn5) and the facial nerve (cn7) and is therefore described in the previous section (Poglayen-Neuwall 1953; Haas 1973).

m. Stylohyoideus (mSty)

The m. Stylohyoideus is innervated by the hyomandibular ramus of cranial nerve 7, the facial nerve (Rieppel 1978). This muscle originates from the distal part of the ceratohyal, and after extending posteriorly it inserts either onto the base of the ceratobranchial (Byerly 1925), or merges with the ventral part of the m. Constrictor Colli (Ruge 1896; Rieppel 1978) (Figure 39).

m. Ceratohyoideus (mCeh)

This muscle is innervated by the glossopharyngeal nerve (cn9) (Rieppel 1978) *contra* Byerly (1925). It is located between the m. Pterygoideus laterally and m. Hyoglossus medially running between the anterior edge of the distal part of the first ceratobranchial and the posterior edge of the ceratohyal (Figure 39) (Rieppel 1978).

m. Geniohyoideus (mGhy)

In general the m. Geniohyoideus (mGen) is a longitudinal muscle found between the lower jaw, first ceratobranchial and entoglossal process (Byerly 1925; Edgeworth 1935; Rieppel 1978; Sch-

wenk 1986). It lies deep to the m. Intermandibularis but superficial to the m. genioglossus (Figures 39 and 40). As Schwenk (1986) described, it does not contribute to the tongue but probably plays a role in supporting it. Its muscle fibres are large in cross-sectional area, a fact that helps distinguish it from neighbouring muscles in the section (Schwenk 1986).

According to (Rieppel 1978) it comprises two parts: a posteromedial m. Geniohyoideus 1 (mGhy 1) and a more lateral m. Geniohyoideus 2 (mGhy 2). There seems to be some uncertainty regarding the exact origins of the different parts (Figure 39), and Schwenk (1986) could not distinguish the two parts at all.

For the squamate *Ctenosaura*, Oelrich (1956) described the innervation of this muscle (=“m. mandibulohyoideus I and II”) as being from the hypoglossal nerve (cn12).

m. Geniohyoideus 1 (mGhy1). The m. Geniohyoideus 1 originates from the lateral surface of the entoglossal process and then extends posterolaterally to insert onto the medial region of the ceratobranchial and the anterolateral edge of the basihyal (Figure 39) (Rieppel 1978). Rieppel (1978) also describes this part as originating from “the midline raphe between the symphysis and the tip of the entoglossal process”; however, in his illustration, this region of the m. Geniohyoideus is labelled as belonging to part 2 (Figure 39).

m. Geniohyoideus 2 (mGhy2). The m. Geniohyoideus 2 originates from the ventromedial surface of the anterior region of the dentary (Figure 39) (Rieppel 1978). As mentioned above this part may also include the fibres that originate from the midline raphe between the symphysis and the tip of the entoglossal process (Rieppel 1978, figure1). Attachment occurs on the anterior edge of the central portion of the first ceratobranchial.

m. Hyoglossus (mHygl)

This muscle has been described many times (Byerly 1925; Lubosch 1933; von Wettstein 1931, 1932; Edgeworth 1935; Rieppel 1978; Schwenk 1986). It is innervated by the hypoglossal nerve (cn12) and originates from the central part of the anterodorsal surface of the first ceratobranchial (Figure 39, 40) (Rieppel 1978). From there it travels anteriorly into the body of the tongue just posterior to the site of the transverse tendinous band (Schwenk 1986). It is possible that some fibres may end ventrally at the band itself (Rieppel 1978) but otherwise this muscle is a continuous column. Coronal histological sections demonstrate that the

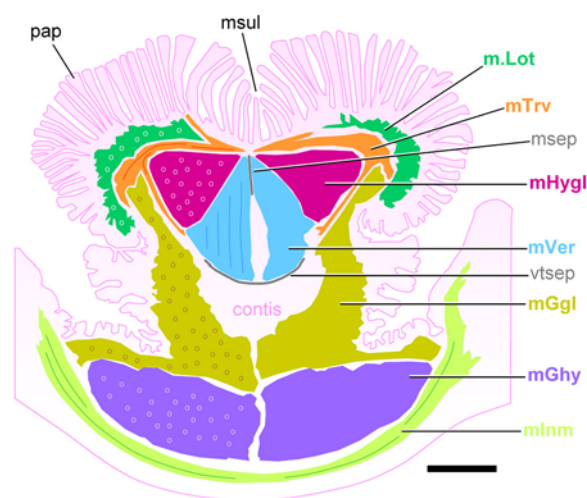


FIGURE 40. A coronal section of the tongue in *Sphenodon* at approximately mid-length. Redrawn and simplified from Schwenk (1986, figure 8). Scale equals 1 mm.

anterior part of the m. Hyoglossus becomes an important component of the tongue situated dorso-laterally to the m. Verticalis and ventral to the m. Transversalis for most of the tongue's length (Figure 39, 40) (Schwenk 1986). In ventral view the hyomandibular artery crosses the muscle from its posterolateral corner towards its anteromedial extent (Figure 33). Contraction of the m. Hyoglossus probably assists retraction of the tongue (Schwenk 1986).

m. Genioglossus (mGgl)

Again this muscle has been examined repeatedly (Byerly 1925; Lubosch 1933; Edgeworth 1935; von Wettstein 1931, 1932; Rieppel 1978; Schwenk 1986). It lies deep to the m. Geniohyoideus (Byerly 1925; Lubosch 1933) and is innervated by the hypoglossal nerve (cn12) (Rieppel 1978). It runs from the anterior end of the throat towards the transverse tendon before contributing significantly to the ventrolateral body of the tongue (Rieppel 1978; Schwenk 1986).

Rieppel (1978) described the origin of the m. Genioglossus as comprising two separate but adjacent anterior heads on the anteromedial surfaces of the lower jaws (Figure 39). The most medial head arises from the midline raphe whereas the lateral head arises from the medial surface of the dentary near the jaw symphysis. Schwenk (1986) observed only a single origin but suggested the difference might be explained by intraspecific variation.

Once within the tongue, muscle fibres of the m. Genioglossus can be observed to travel posteriorly, dorsally, and anteriorly (Schwenk 1986, pers. comm. 2009) both ventral and lateral to the m. Hyoglossus (Figure 40) (Schwenk 1986). Anteriorly fibres from the m. Genioglossus, in conjunction with connective tissue, form the frenulum that attaches the tongue to the floor of the mouth and dorsally some of the fibres mingle with those of the longitudinalis and transversalis (Schwenk 1986).

According to Schwenk (1986, 2000; pers. comm. 2009) contraction of the posterior part of the m. Genioglossus results in tongue protrusion whereas contraction of the anterior part contributes to tongue retraction.

m. Episternohyoid Complex (mEshC)

This complex consists of muscles that insert on the posterior surface of the hyoid (Rieppel 1978). For the squamate *Ctenosaura* Oelrich (1956) described these muscles as being innervated by the first spinal nerve.

m. Omohyoideus (mOmHy). In general the m. Omohyoideus runs parasagittally along the midline (Figure 39) (Rieppel 1978). Originating from the scapulocoracoid ligament and the anteromedial portion of the scapula (Byerly 1925), it inserts into the ventral surface of the posterior part of the basihyal and into the posteroventral edge of the proximal part of the first ceratobranchial (Rieppel 1978).

m. Sternohyoideus (mSteHy). The m. Sternohyoideus (m. Cleidoepesterno Hyoideus in Byerly [1925], m. Episterno-Hyoideus Osawa [1898], Rieppel [1978]) runs deep and obliquely to the m. Omohyoideus so that its anterior part is more laterally positioned (Figure 39) (Rieppel 1978). After originating from the episternum and anterior surface of the medial portion of the clavicle (Byerly 1925) it inserts into the posterodorsal surface of the distal part of the first ceratobranchial (Osawa 1898; Rieppel 1978).

Intrinsic Muscles of the Tongue

The muscles within the tongue have been described primarily by Schwenk (1986) who identified three distinct units: m. Verticalis, m. Transversalis, and m. Longitudinalis (Figure 40). All parts are innervated by the hypoglossal nerve (cn12) (Oelrich 1956).

The tongue itself is fleshy with a shallow midline depression or sulcus (Figure 41.1) (Günther 1867; Gorniak et al. 1982; Schwenk 1986) and is covered in long filamentous papillae, some of which (termed gustatory papillae, Schwenk 1986)

have expanded heads and bear taste buds (Figure 40; Schwenk 1986). Posteriorly it has two “limbs” positioned either side of the glottis and larynx. It is connected to the base of the mouth for almost all of its length (Figure 41.2). Connective tissue forms a significant part of the tongue’s structure, and this must have an important bearing on flexibility and movement (Schwenk 1986). Note that the tip is not forked or bifurcated (Schwenk 1986, 1988 *contra* Gauthier et al. 1988), a condition that supposedly represents the plesiomorphic state for lepidosaurs (Schwenk 1986, 1988).

During protrusion the tongue tip curves ventrally so that the dorsal surface of the foretongue, with its long papillae, is directed toward potential prey items (Schwenk 1986, 2000).

m. Verticalis (mVer). The m. Verticalis is a paired muscle that runs along the central core of the tongue (Figure 39). Anteriorly the left and right portions are generally separated by the median (sagittal) septum but posteriorly the laryngohyoid ligament and entoglossal process also lie between the two portions (Schwenk 1986). Dorsolaterally the m. Verticalis is bounded by the m. Hyoglossus. The anterior portion of the m. Verticalis lies above the m. Genioglossus whereas the posterior portion largely overlies the m. Geniohyoid as the m. Genioglossus become more laterally situated. Osawa (1897) refers to this muscle as the m. Basihyalis Proprius.

m. Transversalis (mTrv). The m. Transversalis extends along the entire length of the tongue. In general it lies near the dorsal surface, above the m. Hyoglossus, but part of it extends ventrally against the lateral surface of the m. Hyoglossus bundle to insert into the ventral transverse septum (Figure 39). A third part extends ventrolaterally into and around the lateral side of the m. Genioglossus bundle. As a result the muscle can look triradiate in coronal section (Schwenk 1986).

m. Longitudinalis (mLot). This m. Longitudinalis (mLot) is a poorly defined set of muscle fibres that runs along the lateral edge of the tongue just beneath the layer of papillae, intermingled with connective tissue (Figure 39). The fibres are most numerous and prominent in the central portion of the tongue, being largely absent from the tip and posterior limbs (Schwenk 1986).

EXTRINSIC MUSCLES OF THE SKULL AND PECTORAL GIRDLE

The extrinsic muscles are those that connect the skull to either the axial or appendicular skele-

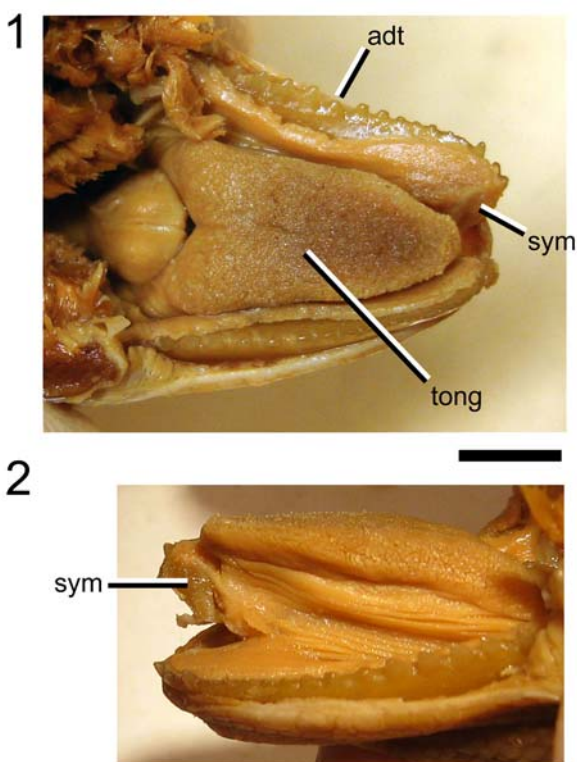


FIGURE 41. The tongue of a subadult *Sphenodon* (BMNH 1972.1223) in dorsal view (41.1) and left lateral view with the left mandible disarticulated and moved downwards out of the way (41.2). Scale equals 5 mm.

ton. These muscles are associated with the pectoral girdle and neck. Muscles from the pectoral girdle that link the skull to the appendicular skeleton include the m. Trapezius, the m. Episternocleidomastoid, and the m. Clavicle Dorsalis (Byerly 1925; Al-Hassawi 2004, 2007). All three muscles are innervated by branches of the second, third, and fourth spinal nerves (Byerly 1925). For information regarding other muscles of the pectoral girdle such as the m. Levator Scapulae, readers are directed towards Günther (1867), Osawa (1898), Byerly (1925), von Wettstein (1931), and Al-Hassawi (2004, 2007).

m. Trapezius (MTrap)

The m. Trapezius is a wide sheet-like muscle that connects the shoulder girdle to the skull and vertebral column and serves to protract the forelimb (Byerly 1925). It originates from the fascia and fatty tissue along the crest of the vertebral column (Byerly 1925; Edgeworth 1935; Al-Hassawi 2004, 2007) but here we are most concerned with the anteriormost point of origin that is closest to the back of the skull. According to Byerly (1925) this

comprises an origin from the parietal-squamosal arch superficial to the m. Depressor Mandibulae (Figures 21, 22 and 42). Similarly, Al-Hassawi (2004, 2007) described the site of origin as the fatty tissue and muscle fascia on the posterodorsal margin of the skull but she does not consider the area of origin to include the midline (*contra* Byerly 1925). Tsuihiji (2007, p. 1011) describes the m. Trapezius (within a muscle group he called the m. Cucullaris Complex) as originating from the posterior surface of the parietal and squamosal between the m. Depressor Mandibulae and m. Longissimus Capitis, but he is probably referring to part of the m. Episternocleidomastoid or m. Clavicle Dorsalis rather than the m. Trapezius of other authors.

Al-Hassawi (2004, 2007, p. 105) describes the m. Trapezius as inserting on the anterior half of the dorsal edge of the clavicle. Byerly (1925, p. 24) instead describes this muscle as inserting on the dorsal third of the anterior border of the scapula (Figure 43).

m. Episternocleidomastoid (mEscm)

The m. Episternocleidomastoid serves to lift the scapula, but may also be used when moving the head. For this extrinsic muscle Byerly (1925) uses the term “cephalo-clavicularis” whereas Tsuihiji (2007) refers to it within the “m. Cucullaris complex.”

The muscle originates from the anterior margins of the clavicle and interclavicle ventral to the insertion of the m. Trapezius (Figures 21, 22, 43, 44, and 45) (Byerly 1925; Al-Hassawi 2004, 2007; Tsuihiji 2007). Al-Hassawi (2004, 2007) described three separate insertions on the posterior surface of the skull:

- Branch 1 (mEscm1). Inserts on the posterolateral end of the paroccipital processes of the opisthotic (Figure 42).

- Branch 2 (mEscm2). Inserts above branch 1 on the posteromedial margin of the squamosal just above the contact with the paroccipital process of the opisthotic (Figure 42).

- Branch 3 (mEscm3). Inserts along the posterodorsal edge of the squamosal and parietal immediately ventral to the origin of the m. Depressor Mandibulae and dorsal to the m. Semispinalis Capitis. According to the figure provided by Al-Hassawi (2004, 2007, p. 117, figure 3.4a) the area of insertion for this branch is double the size of that for branches 1 and 2 (Figure 42).

As Tsuihiji (2007) points out, Fürbringer (1900) also reported that a portion of this muscle may insert on the quadratojugal.

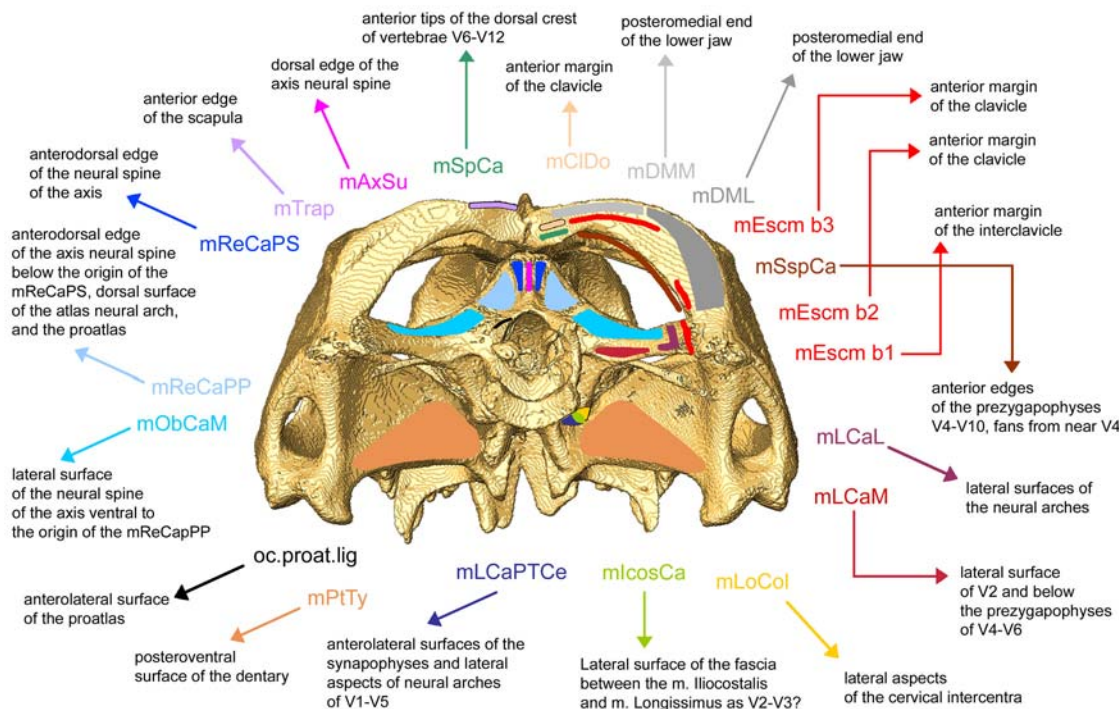


FIGURE 42. Skull model of *Sphenodon* (LDUCZ x036), generated using micro CT data, in posterior view labelled with areas of muscle attachment. Compiled with information from direct observations in conjunction with Al-Hassawi (2004, 2008) and Tsuihiji (2005, 2007).

m. Clavicle Dorsalis (mClDo)

The m. Clavicle Dorsalis originates from the anterolateral surface of the clavicle dorsal (Figures 21, 22, 43, and 44) to the m. Episternocleidomastoid and it inserts onto the posterior surface of the parietal medial to the insertions of the m. Episternocleidomastoid (Figures 21, 22, and 42). It lies beneath m. Depressor Mandibulae and m. Trapezius (Al-Hassawi 2004, 2007). Byerly (1925) probably included this muscle as part of the “cephaloclavicularis” whereas Tsuihiji (2007) included it within the “cucullaris complex.”

EXTRINSIC MUSCLES OF THE SKULL AND NECK

The axial muscles of the neck can be divided into epaxial muscles that run above the ribs and hypaxial muscles that run below the ribs (Gasc 1981; Tsuihiji 2005, 2007). The epaxial muscles are further divided into three groups, all of which broadly run parallel to the vertebral column (Nishi 1916; Gasc 1981; Tsuihiji 2005):

1. m. Transversospinalis (medial column)
2. m. Longissimus (central column)

3. m. Iliocostalis (lateral column)

In general, the m. Transversospinalis sits against the neural spines, the m. Longissimus sits alongside the zygapophyses of the vertebrae, and the m. Iliocostalis is positioned on top of the ribs. The m. Transversospinalis, and more lateral m. Longissimus are separated by the fascial “septum intermusculare dorsi” (Nishi 1916; Tsuihiji 2005), but m. Longissimus and m. Iliocostalis are not clearly divided by fascia in *Sphenodon* (Nishi 1916; Tsuihiji 2005). These three groups can also be defined based on their innervation because they receive different twigs or branches from the dorsal rami of the segmental spinal nerves (Gasc 1981; Tsuihiji 2005).

The axial muscles of *Sphenodon* have been described several times (Maurer, 1896; Osawa 1898; Nishi 1916; Byerly 1925; von Wettstein 1931; Gasc 1981; Tsuihiji 2005, 2007; Al-Hassawi 2004, 2007). In his study of non-avian reptile axial musculature, Gasc (1981) dissected at least one specimen of *Sphenodon* in addition to other taxa. Byerly (1925) described some of the neck and shoulder muscles as part of his more general description of the muscles in *Sphenodon*. The von Wettstein article (1931) is a review of previous work, whereas

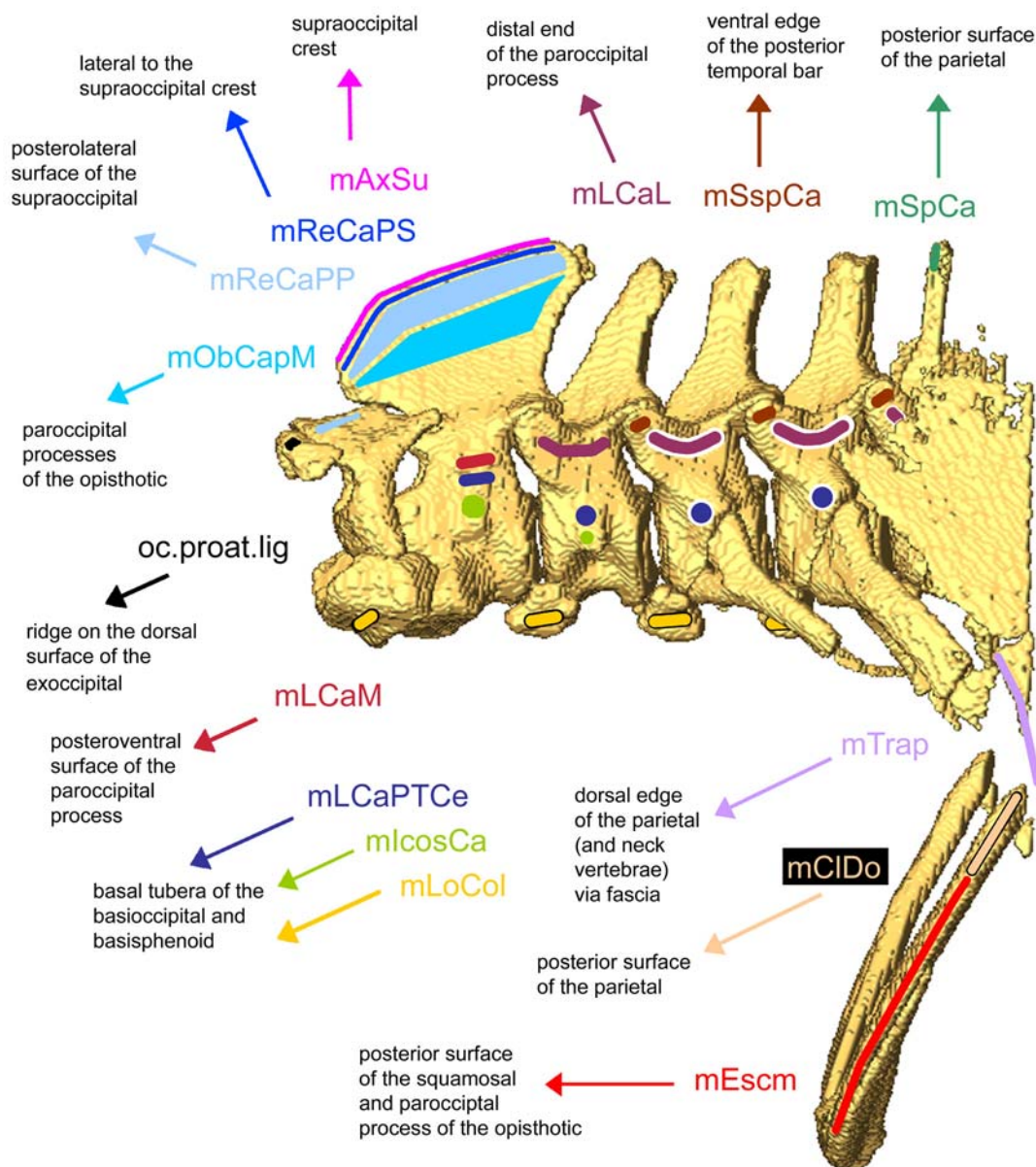


FIGURE 43. Neck model of *Sphenodon* (YPM 9192), generated using micro CT data, in left lateral view, labelled with areas of muscle attachment. Compiled with information from direct observations in conjunction with Al-Hassawi (2004, 2008) and Tsuihiji (2005, 2007).

Al-Hassawi (2004, 2007) specifically concentrated on the cervical muscles in lepidosaurs and partially dissected one *Sphenodon* specimen. In two detailed works regarding axial muscles in reptiles, Tsuihiji (2005, 2007) dissected part of one *Sphenodon* specimen (listed as specimen CAS 20888, SVL 250 mm).

For information regarding the muscles of the neck that do not attach to the skull, such as the intercentral muscle slips, readers are directed

towards Günther (1867), Maurer (1896), Osawa (1898), Nishi (1916), Byerly (1925), von Wettstein (1931), Gasc (1981), Al-Hassawi (2004, 2007), and Tsuihiji (2005, 2007).

Spinalis (mSp)

The m. Spinalis is a bundle of muscle and tendons within the m. Transversospinalis group (the most medial column of the epaxial muscles) that runs broadly parallel to the vertebral column along-

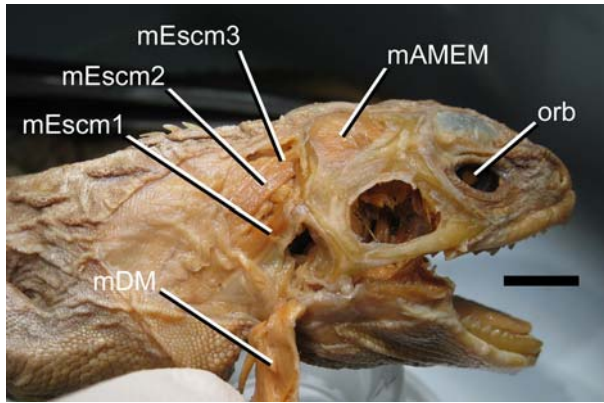


FIGURE 44. Subadult *Sphenodon* specimen (BMNH 1972.1223) in right lateral view showing the different branches of the m. Episternocleidomastoid. Scale equals 10 mm.

side the neural spines (Nishi 1916; Gasc 1981; Tsuihiji 2005). It is innervated by medial branches of the dorsal rami of the spinal nerves (Nishi 1916; Gasc 1981; Tsuihiji 2005). Anterior portions of this muscle group connect the axial column to the back of the skull and are presumably used to support and lift the head. These muscles include the m. Spinalis Capitis and the more laterally positioned m. Semispinalis Capitis. However, these muscles are interconnected and difficult to separate from the rest of the m. Spinalis (Tsuihiji 2005).

Spinalis Capitis (mSpCa). The m. Spinalis Capitis connects the vertebral column to the skull via tendons that arise from the neural spines (Figures 21, 22, 23, and 43) (Nishi 1916; Tsuihiji 2005). This muscle is probably equivalent to the “semi-spinalis

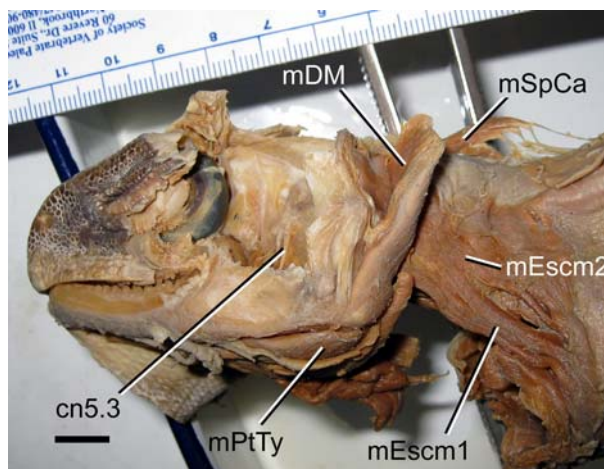


FIGURE 45. *Sphenodon* head and neck (BMNH 1969.2204) in left lateral view showing parts of the m. Depressor Mandibulae, m. Episternocleidomastoid and the m. Spinalis Capitis. Scale equals 10 mm.

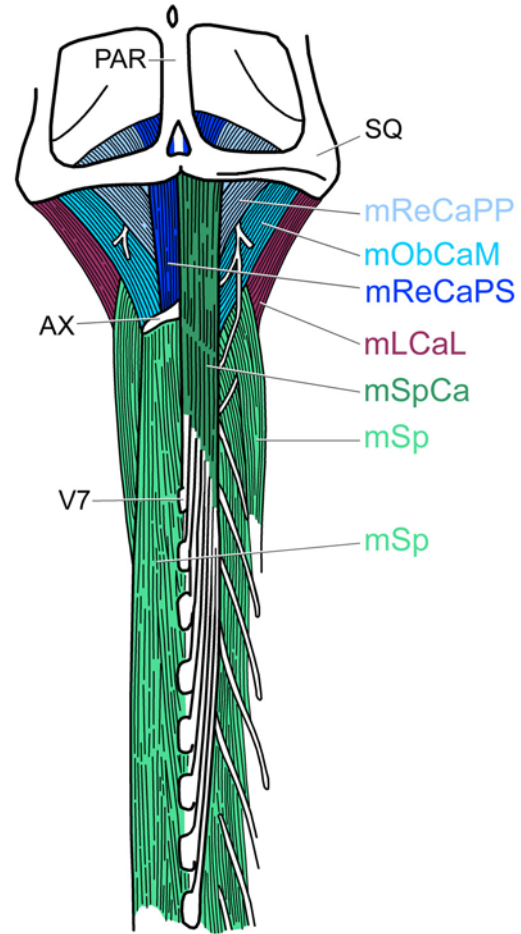


FIGURE 46. Central neck muscles of *Sphenodon* in dorsal view with the m. Spinalis Capitis removed from the left side and m. Semispinalis capitis removed from both sides. Redrawn from Nishi (1916).

capitis” of Byerly (1925, p. 18). The tendons insert on the posterior surface of the parietal near the midline deep to the m. Depressor Mandibulae and extrinsic muscles of the pectoral girdle (Figure 42) (Byerly 1925; Al-Hassawi 2004, 2007; Tsuihiji 2005). According to Byerly (1925) the muscle originates on the anterolateral edges of the neural spines between the 4th and 8th vertebrae before inserting on the posterior surface of the parietal. In specimen BMNH 1969.2204 the anteriormost origination, via a tendon, is from the 7th vertebra (Figures 23 and 45). This corresponds to the work by Nishi (1916, p. 261) (Figure 46).

Semispinalis Capitis (mSspCa). As Tsuihiji (2005) points out, the m. Semispinalis Capitis muscle was originally described as the m. Semispinalis Dorsi by Nishi (1916) and corresponds to the “articulo-parietalis” of Olson (1936), and probably to the

“Cervico-capitis” of Byerly (1925, p. 19), and Longissimus capitis 1 of Al-Hassawi (2004, 2007). Tsuihiji (2005) argues that it should not be considered part of the longissimus muscles and instead has a closer relationship to the spinalis muscles.

This muscle connects the vertebral column to the skull and originates via tendons from the prezygapophyses (Tsuihiji 2005). According to Al-Hassawi (2004, 2007) this muscle branches from the m. Longissimus Dorsi near the 7th vertebra and inserts on the posterior ventral edge of the parietal and squamosal (Figures 42 and 43). In specimen BMNH 1972.1223 this muscle can be seen deep to the m. Depressor Mandibulae and m. Episternocleidomastoid (Figure 47). It fans anterolaterally from the axial column and inserts on the posteroverventral edge of the parietal-squamosal bar.

Splenius Capitis (mSpICa)

The “splenius capitis” of Al-Hassawi (2004, 2007) follows a very similar path to the m. Spinalis Capitis along the dorsal part of the vertebral column. It inserts on the posterior surface of the parietal just dorsal to the m. Spinalis Capitis (Al-Hassawi (2004, p. 66, 2007, p. 66) and origination is via tendinous bundles from the tips of the neural spines of the 6th to 12th vertebrae (Al-Hassawi 2004, p. 107, 2007, p. 107). Tsuihiji (2005) probably includes this muscle within the m. Spinalis Capitis.

Axis-Supraoccipital (mAxSu)

The m. Axis-Supraoccipital originates from the atlantal neural arch and also the anterodorsal margin of the axis and travels anteriorly to insert on the posterodorsal crest of the supraoccipital (Figures 42, 43 and 48) (Al-Hassawi 2004, 2007). It probably serves to support and lift the head. This muscle was identified by Al-Hassawi (2004, 2007) and is apparently not known in any other taxon. However, she does not discuss whether this muscle may simply be part of the Rectus Capitis (mReCa). Tsuihiji (2005) does not describe any muscle fibres that might represent the m. Axis-Supraoccipital so its presence may be subject to individual variation. Examination of BMNH 1969.2204 suggests that what Al-Hassawi (2004, 2007) observed is probably a tendinous sheet and not a muscle.

Rectus Capitis (mReCa)

The m. Rectus Capitis contributes to lateral movements of the head (Byerly 1925). It originates from the atlantal arch and anterodorsal part of the neural spine of the axis (Figures 43 and 46) and

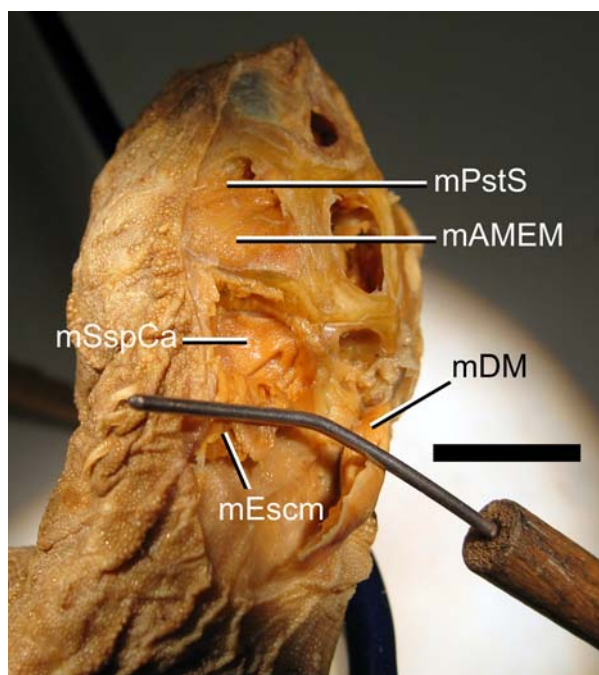


FIGURE 47. Subadult *Sphenodon* head (BMNH 1972.1223) in posterodorsal view showing the fan shaped m. Semispinalis Capitis. The overlying m. Episternocleidomastoid and m. Depressor Mandibulae have been folded back on the right side. Scale equals 10 mm.

inserts on the posterior surface of the braincase (Figures 34 and 42) (“rectus capitis posticus” in Byerly 1925; Al-Hassawi 2004, 2007; Tsuihiji 2005). Based on dissection of specimen CAS20888 Tsuihiji (2005) divided the m. Rectus Capitis into a superficial and deep portion with the superficial portions inserting more medially. This confirmed observations made by Nishi (1916). The cranial portion of this muscle is still present on the right side of specimen BMNH 1969.2204.

Rectus Capitis Posterior Superficialis (mReCaPS). The m. Rectus Capitis Posterior Superficialis originates from the anterodorsal portion of the lateral surface of the axis neural spine (Figures 43 and 46) (Nishi 1916; Tsuihiji 2005). Tsuihiji (2005) described the insertion as being lateral to the posterodorsal midline crest of the supraoccipital (Figure 42). Neither Al-Hassawi (2004, 2007) or Tsuihiji (2005) report insertions on the squamosal in contrast to Byerly (1925). In specimen BMNH 1969.2204 the muscle is about 5 mm high and 1 mm wide at mid section.

m. Rectus Capitis Posterior Profundis (mReCaPP). This muscle originates on the anterodorsal edge of the lateral surface of the axis neural spine

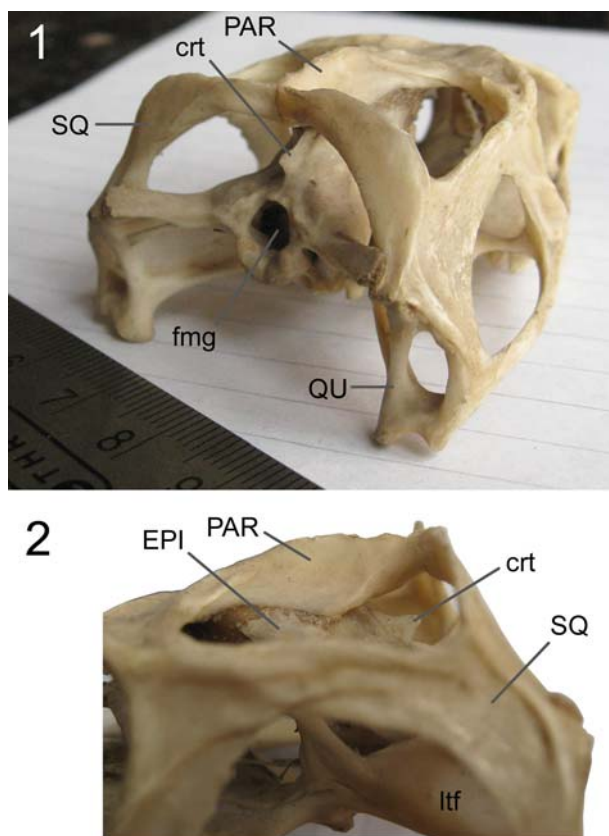


FIGURE 48. The posterodorsal crest on the supraoccipital in *Sphenodon* (large apparently unregistered specimen in the Zoology collection of Ernst Moritz Arndt University, Greifswald) viewed in anterolateral aspect (48.1) and left lateral aspect (48.2). According to Al-Hassawi (2004, 2007) the supraoccipital crest is where the m. Axis-Supraoccipital attaches. The crest projects posterodorsally approximately 4 mm.

ventral to the origin of the m. Rectus Capitis Posterior Superficialis and also from the dorsal surface of the atlas and proatlas (Figures 43 and 46) (Nishi 1916; Tsuihiji 2005). Insertion takes place on the posterolateral surface of the supraoccipital lateral to the m. Rectus Capitis Posterior Superficialis (Figures 34, 42 and 46) Tsuihiji (2005). The lateral-most part of this insertion is associated with a shallow ridge (Al-Hassawi 2004, 2007). This is confirmed by examination of specimen BMNH 1969.2204. In mid section the muscle is about 4 mm wide and less than 1 mm high.

m. Obliquus Capitis Magnus (mObCaM)

The m. Obliquus Capitis Magnus is a flat muscle that spans the gap between the lateral surface of the axis and the posterodorsal surface of the paroccipital process of the opisthotic (Figures 42

and 46) (Nishi 1916; Al-Hassawi 2004, 2007; Tsuihiji 2005). Its origin is ventral to that of the m. Rectus Capitis whereas its insertion is more lateral to that of the m. Rectus Capitis. A dorsal branch of the dorsal cervical plexus lies between the m. Obliquus Capitis and m. Rectus Capitis (Nishi 1916; Tsuihiji 2005).

Al-Hassawi (2004, 2007) reported that the origin took place on the axis neural arch whereas Tsuihiji (2005) reported the origin as being the lateral surface of the axis neural spine. The “Obliquus Capitis” of Byerly (1925) probably corresponds to parts of the m. Longus Capitis and m. Semispinalis Capitis. This muscle is probably partly responsible for lateral head movements and also lifting of the head.

In specimen BMNH 1969.2204 a strap-shaped muscle can be seen to insert on the dorsal surface of the paroccipital process of the opisthotic (Figure 34). In section it is approximately 7 mm wide and 2 mm high. This muscle may be the anterior portion of the m. Obliquus Capitis Magnus.

m. Longissimus (mL)

The m. Longissimus is the central column of the epaxial muscles that runs parallel to the vertebral column, alongside the zygapophyses of the vertebrae, medial to the iliac blade (Nishi 1916; Gasc 1981; Tsuihiji 2005). The muscle group is innervated by medial twigs of the lateral branches of the dorsal rami of the spinal nerves (Tsuihiji 2005). The main part of this muscle (often referred to as the m. Longissimus Dorsi) originates from the ilium and sacrum, and runs anteriorly towards the skull along the lateral surface of the zygapophyses (Al-Hassawi 2004, 2007). The m. Longissimus cervicis branches away from this muscle and bifurcates into two heads. The anterior head inserts on the proatlas whereas the posterior head inserts on the posterior process of the atlas. Two other muscles branch off from the m. Longissimus and attach to the back of the head: the m. Longissimus Capitis Lateralis (mLCaL) and m. Longissimus Capitis Medialis (mLCaM).

m. Longissimus Capitis Lateralis (mLCaL). This muscle is equivalent to the Longissimus capitis 2 (mLongiC2) of Al-Hassawi (2004, 2007, p. 100) and the lateral most part of the “m Transversalis Cervicis” of Nishi (1916, p. 261). It branches from the m. Longissimus Dorsi (mLD), near the 3rd vertebra and inserts on the lateral tip (or most distal end) of the paroccipital process of the opisthotic (Al-Hassawi 2004, 2007). The area of insertion illustrated by Tsuihiji (2005, figure 4) for the “m. Longis-

simus Capitis pars transversalis” is in agreement with this (Figures 42 and 43). Evidence of this attachment appears to be present in BMNH 1969.2204.

m. Longissimus Capitis Medialis (mLCaM). This muscle is equivalent to the Longissimus capitis 3 (mLongiC3) of Al-Hassawi (2004, 2007, p. 100). It branches from the m. Longissimus Dorsi at a point near the axis (Al-Hassawi 2004, 2007), and inserts along the posterior surface on the paroccipital process of the opisthotic below the insertion of the m. Obliquus Capitis Magnus (Al-Hassawi 2004, 2007). The area of insertion illustrated by Tsuihiji (2005, figure 4) for the “m. Longissimus Capitis pars transversalis” is in agreement with this (Figures 42 and 43).

m. Longissimus Capitis Pars Transversalis Cervicus (mLCaPTCe). This muscle probably corresponds to the “Longissimus capitis 4” (mLongiC4) of Al-Hassawi (2004, 2007, p. 100), which she describes as branching from the m. Longissimus Dorsi near the 2nd vertebra (axis) and inserting on the posterolateral epiphyses of the basal tubera of the basioccipital (Figures 14, 42, 43, 49, and 50). This corresponds with the descriptions of Tsuihiji (2007) for the “m Longissimus Capitis Pars Transversalis Cervicus.” The cranial portion of this muscle is present on the right side of BMNH 1969.2204 and is triangular in mid-section (Figure 34): the dorsal edge is 4 mm wide whereas the ventrolateral edge and ventromedial edges are both about 6 mm long.

Iliocostalis (mlcos)

The m. Iliocostalis is the lateral column of the epaxial muscles which runs broadly parallel to the vertebral column, on top of the ribs and lateral to the iliac blade (Nishi 1916; Gasc 1981; Tsuihiji 2005). The muscle group is innervated by lateral twigs of the lateral branches of the dorsal rami of the spinal nerve (Tsuihiji 2005). The m. Iliocostalis capitis is the part of this muscle that connects the axial skeleton to the head.

Iliocostalis capitis (mlcosCa). The m. Iliocostalis capitis supposedly originates from the rest of the iliocostalis at about the level of the second and third vertebrae from the fascia separating the m. Iliocostalis and m. Longissimus (Figure 43) (Tsuihiji 2007). It inserts on the basal tubera of the basioccipital anterolateral to the insertions of the m. Longus Capitis Pars Transversalis Cervicus and m. Longus Colli (Figures 14, 42, 43, 49, and 50) (Tsuihiji 2007). In BMNH 1969.2204 a muscle that

probably represents the cranial half of the m. Iliocostalis capitis is about 2 mm tall by 1 mm wide in section.

m. Longus Colli (mLoCol)

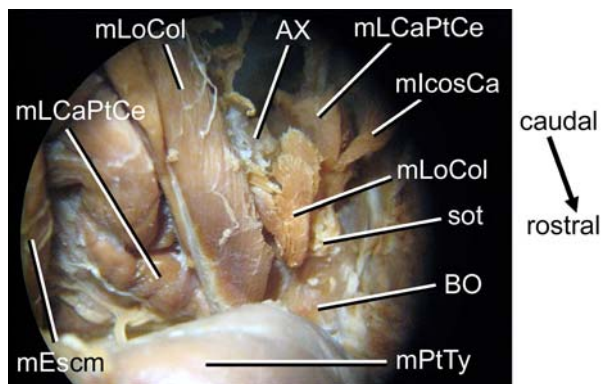
The m. Longus Colli is the subvertebral layer of the hypaxial musculature. It arises from a series of slips along the base of the vertebral column that converge into a single bundle that inserts on the ventral surface of the braincase (Figures 14, 22.2, 42, 43, 49, 50, and 51) (Osawa 1898; Byerly 1925; Gasc 1981; Al-Hassawi 2004, 2007; Tsuihiji 2007). Tsuihiji (2007) considers the m. Longus Colli of *Sphenodon* to include the m. Rectus Capitis of other diapsids. As a result he occasionally refers to the m. Longus Colli as the m. Rectus Capitis (e.g., Tsuihiji 2007, figure 4).

Byerly (1925, p. 18) described the insertion as being on the ventral surface of the axis and occipital condyle. Other authors describe its insertion as taking place on the sphenoccipital tubercle (basal tubercle) of the basisphenoid via a tendon medial to the insertions of the m. Iliocostalis Capitis and the m. Longus Capitis Pars Transversalis (Osawa 1898; Byerly 1925; Al-Hassawi 2004, 2007; Tsuihiji 2007).

There is some disagreement with regards to the precise origins of this muscle. Byerly (1925, p. 17) described it arising from the ventral surfaces of 2nd to 12th vertebrae with an additional slip coming from the rib of the seventh vertebra. Osawa (1898) also considered some fibres to originate from the atlas. Al-Hassawi (2004, 2007) described the posteriormost part of this muscle as originating from the 11th intercentrum (between the 10th and 11th vertebrae) and comprising three subdivisions:

1. A superficial section from intercentrum 8 (equivalent to the 6th keeled intercentrum) between the 7th and 8th vertebrae. It eventually joins the 2nd section.
2. An intermediate section from the flat 10th intercentrum (between the 9th and 10th vertebrae).
3. A third section from the 11th intercentrum (between the 10th and 11th vertebrae) extends laterally to join the other two sections.

Al-Hassawi (2004, 2007, p. 100) also describes two further slips that are probably part of the m. Longus Colli: “first flat intercentral muscle slip to the basioccipital” and “third intercentral muscle slip to the basioccipital.”



held up, but its placement below the occipital condyle suggests it is better suited for moving the head down.

Sphenodon is the best available outgroup for inferring soft tissue homologies and soft tissue character polarity in squamates (e.g., Schwenk 1986; Bryant and Russell 1992; Witmer 1995, 1997; Abdala and Moro 2003; Tsuihiji 2005, 2007; Holliday and Witmer 2007). However, *Sphenodon*'s status as a representative of the ancestral condition must be approached with caution as squamates and rhynchocephalians separated from one another approximately 240-250 million years ago (Evans 2003; Vidal and Hedges 2005; MEHJ unpublished data), and *Sphenodon* is certainly not representative of Rhynchocephalia as a whole (e.g., Evans 1980; Whiteside 1986; Fraser 1988; Reynoso 2000; Apesteguía and Novas 2003; Jones 2008). Incidentally, it is not correct to refer to Rhynchocephalia as being basal to Squamata (e.g., Reilly et al. 2001, p. 403) because, by definition as sister taxa, both groups originated at the same time (Evans 2003; MEHJ unpublished data). Correspondingly, Squamata can be used as an outgroup for Rhynchocephalia, and *Sphenodon* is not "the most basal member of the extant lepidosaurs" (*contra* Tsuihiji 2005, p. 176; see Baum et al. 2005). Despite frequent claims to the contrary (e.g., Sharell 1966; Crook 1975; Dawbin 1982; Daugherty and Cree 1990; Finch and Lambert 1996; Pough et al. 2005; Alibardi and Toni 2006; Reilly et al. 2006), there is very little direct evidence that *Sphenodon* has remained "unchanged" for 140 million years or more (Whiteside 1986;

FIGURE 49. The junction between the head and neck in *Sphenodon* (BMNH 1969.2204). Shows the attachment of the m. Longissimus Capitis Pars Transversalis Cervicus, m. Iliocostalis Capitis and m. Longus Colli onto the basal tubera of the basioccipital. On the left hand side muscles such as the m. Longus Colli and m. Pterygoideus Typicus have been dissected away entirely. Scale equals 5 mm.

Examination of BMNH 1969.2204 confirms the presence of a tendon into which the slips converge (Figures 49 and 50), that the intercentra are an important site of origin (Al-Hassawi 2004, 2007), and that the most anterior point of origin includes the first intercentrum (Al-Hassawi 2004, 2007).

Byerly (1925) considered this muscle important for moving the head sideways and keeping it

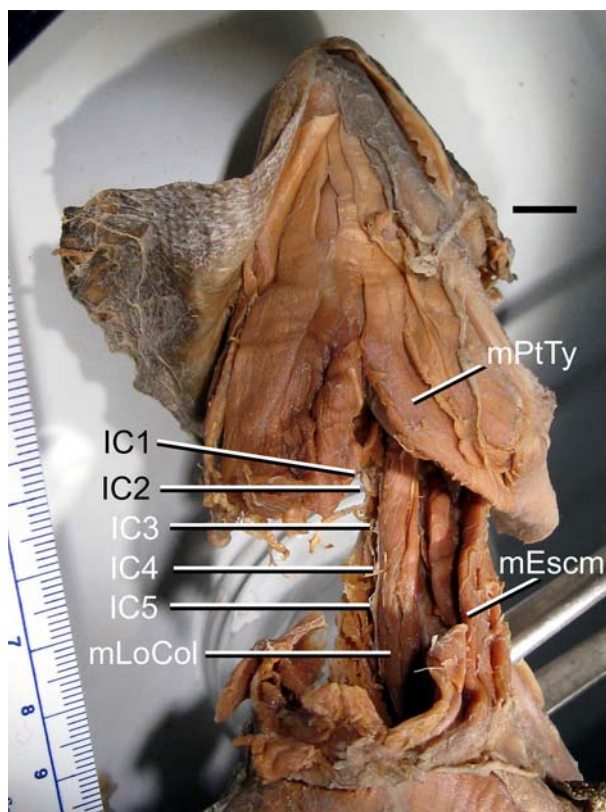


FIGURE 51. *Sphenodon* head and neck in ventral view (BMNH 1969.2204) demonstrating the position of the left m. Longus Colli. Scale equals 10 mm.

Jones 2008, Jones et al. 2009; Evans and Jones in press). *Sphenovipera*, from the Early Jurassic of Mexico, known from a single lower jaw (Reynoso 2005), has *Sphenodon*-like dentary teeth but the proportions of the lower jaw are notably different. Its adductor fossa is very short, suggesting its temporal region was also short. The most plesiomorphic rhynchocephalians, such as *Diphydontosaurus* from the Triassic of England, appear to have employed some kind of propalinal jaw movement as in *Sphenodon* (Evans 1980; Fraser 1982; Whiteside 1986; Jones 2008), but differences in skull shape suggest that they may have differed in muscle arrangement (Evans 1980; Whiteside 1986; Jones 2008).

Here we have provided an up-to-date overview of the head and neck musculature with novel contributions from direct examinations of wet material. The musculature is complicated and composed of several distinct groups themselves amenable to further subdivision (e.g., Figures 13, 21, 22, 42, and 43).

Several aspects of the muscle arrangement are interesting from a functional point of view, for

example, the fact that the large m. Adductor Mandibulae Externus Superficialis attaches to a strong sheet of fascia held within the lower temporal fenestra (Figure 20). This has previously attracted little attention but in other circumstances it has been noted that where skeletal structures are in net tension through all functional loadings, bone is often replaced by ligament or membrane (Oxnard et al. 1995; Witzel and Preuschoft 2005) whereas net compression ensures bone deposition (Gregory and Adams 1915; Adams 1919; Case 1924; Olsen 1961). It is possible that the lower temporal fenestra (and fascia) exists because there is net tension as a result of the functioning of the m. Adductor Mandibulae Externus Superficialis (when the lower jaw meets resistance). Another point of interest involves the position of the m. Pterygoideus Atypicus (Figures 31 and 37). Because the vertebrate jaw joint is usually closer to the jaw muscles than are the teeth contacting the prey item, joint reaction forces are expected to be higher than those resulting from the bite. It has been argued that mammals reduce this problem by the development of an anteriorly placed masseter muscle (Crompton and Parker 1978; Russell and Thomason 1993, p. 351). The m. Pterygoideus Atypicus in *Sphenodon*, and other reptiles that possess it, may similarly offset reaction force to some extent.

As previously described, the tongue morphology of *Sphenodon* is very similar to that of iguanian squamates (Oelrich 1956; Schwenk 1986, 1988; Smith 1988). Cladistic analyses based on morphological data (e.g. Estes 1988; Conrad 2008) suggest this shared tongue morphology may represent the ancestral condition for lepidosaurs. By contrast, phylogenetic topology based on molecular data (Townsend et al. 2004; Vidal and Hedges 2005) favour this tongue morphology having been acquired independently by *Sphenodon* and iguanians. Extinct rhynchocephalians demonstrate different palatal tooth arrangements compared to *Sphenodon* that may also reflect differences in tongue structure (Jones 2008).

Discrepancies in previous descriptions with regards to the details of origins and insertion are probably due to a number of factors including specimen quality, descriptive accuracy, and criteria for homology (e.g., see Haas 1973, p. 293-296). The problem is exacerbated by mistakes such as those found in the figure labelling of Haas (1973), Holli-day and Witmer (2007) and possibly Gorniak et al. (1982). Nevertheless, individual variation is probably a 'real' and significant factor (Ostrom 1962;

Haas 1973; Wu 2003). In fact, individual variation is probably greater than reported because when confronted by uncertain morphology authors may, on occasion, have chosen to follow previous descriptions. The level of intraspecific variation in muscle structure found in *Sphenodon* may be no greater than that in any other taxon, being evident only because of the number of descriptions carried out. Alternatively the isolated island existence may have allowed intraspecific variation to increase under relaxed selection pressures (Whiteside 1986, p. 425). Ostrom (1962) suggested that individual variation might be related to environmental factors such as favoured diet but Haas (1973) considered ontogeny to be the main contribution to morphological variation.

To reduce the possibility of future misunderstandings we advise that further descriptions of muscle arrangement in reptiles should use previously established colour coding schemes and abbreviation formatting (e.g., Holliday and Witmer 2007; Tsuihiji 2005, 2007) as far as possible.

The work presented here will form the basis of future computer modelling work (e.g., Curtis et al. 2008; Moazen et al. 2008, 2009) to evaluate the complex relationships between muscle arrangement and skull shape in diapsid reptiles.

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ABBREVIATIONS APPENDIX

Abbreviations in alphabetical order. Bones are in capital letters, muscles are a mixture of capital letters and lower case, whereas features are all in lower case. Combinations of abbreviations may be separated by a full stop (e.g., low.pr), in such combinations abbreviations for bones are not capitalized (e.g., mx.fct).

add.cha	adductor chamber
add.fos	adductor fossa of the lower jaw
adt	additional tooth
AN	ANGULAR
apmx	anterior process of the maxilla
ART	ARTICULAR
art.sur	articular surface
AT	ATLAS
AX	AXIS
BO	BASIOCCIPITAL
bpr	basipterygoid processes
BS	BASISPHENOID
BSHL	BASIHyal
can	caniniform
ce	centrum
chi	chisel-like tooth
cho	choana (internal nares)
CL	CLAVICLE
cn5.1	ophthalmic division of cranial nerve 5 (trigeminal)
cn5.2	maxillary division of cranial nerve 5 (trigeminal)
cn5.3	mandibular division of cranial nerve 5 (trigeminal)
cn5.3mh	mylohyoid branch of cranial nerve 5 (trigeminal)
cn7hy	hyomandibularis branch of cranial nerve 7 (facial)
cn9	cranial nerve 9 (glossopharyngeal)
cn12	cranial nerve 12 (hypoglossal)
CO	CORONOID
contis	connective tissue
cpd	coronoid process of the dentary
CRB1	CERATOBANCHIAL 1

CRB2	CERATOBANCHIAL 2
CRHL	CERATOHYAL
crt	crest
DEN	DENTARY
dep	depression
ECPT	ECTOPTERYGOID
ent.pr	entoglossal process
epiph	epiphyses
EPT	EPIPTERYGOID
EXOC	EXOCCIPITAL
fas	fascia
fct	facet
fl	flange
fmg	foramen magnum
fn	fontanelle
for	Foramen
fpmx	facial process of the maxilla
FR	FRONTAL
gcn5.1	ophthalmic ganglion
gmm	maxillomandibular ganglion
hatch	hatchling teeth
hma	hyomandibular artery
IC1	INTERCENTRUM 1
IC2	INTERCENTRUM 2
IC3	INTERCENTRUM 3
IC4	INTERCENTRUM 4
ICL	INTERCLAVICLE
ios	interorbital septum
iptv	interpterygoid vacuity
ise	interdigitated seam
jj	jaw joint
JUG	JUGAL

ke	keel
ld	lacrimal duct
lig	ligament
ltb	lower temporal bar
ltf	lower temporal fenestra
m	musculus
mPPt	m. Protractor Pterygoidei
mAME	m. Adductor Mandibulae Externus
mAMEM	m. Adductor Mandibulae Externus Medialis
mAMEMa	ventrolateral head of the m. Adductor Mandibulae Externus Medialis
mAMEMb	anteromedial head of the m. Adductor Mandibulae Externus Medialis
mAMEMc	posterior head of the m. Adductor Mandibulae Externus Medialis
mAMEP	m. Adductor Mandibulae Externus Profundus
mAMES	m. Adductor Mandibulae Externus Superficialis
mAMI	m. Adductor Mandibulae Internus
mAMP	m. Adductor Mandibulae Posterior
man.for	mandibular foramen
max.tr	maxillary tooth row
mAxSu	Axis-supraoccipital muscle
mAxSu	m. Axis-supraoccipital
mCCol	m. Constrictor Colli
mCeh	m. Ceratohyoideus
mCID	m. Constrictor Internus Dorsalis
mCIDo	m. Clavicle Dorsalis
mDM	m. Depressor Mandibulae
mDML	m. Depressor Mandibulae Lateralis
mDMM	m. Depressor Mandibulae Medialis
mEscm	m. Episternocleidomastoid
mEscm1	m. Episternocleidomastoid branch 1 (ventral most)
mEscm2	m. Episternocleidomastoid branch 2
mEscm3	m. Episternocleidomastoid branch 3 (dorsal most)

mar	mandibular artery
mf	maxillary foramen
mGgl	m. Genioglossus
mGhy	m. Geniohyoideus
mGhy1	m. Geniohyoideus 1 (medial part)
mGhy2	m. Geniohyoideus 2 (lateral part)
mHygl	m. Hyoglossus
mlcos	m. Iliocostalis
mlcosCa	m. Iliocostalis capitis
mlnm	m. Intermandibularis
mkgr	meckelian groove
mL	m. Longissimus
mLBul	m. Levator Bulbi
mLCaL	m. Longissimus Capitis Lateralis
mLCaM	m. Longissimus Capitis Medialis
mLCaPTCe	m. Longus Capitis Pars Transversalis Cervicus
mLoCol	m. Longus Colli
mLot	m. Longitudinalis
mLPt	m. Levator Pterygoidei
mObCaM	m. Obliquus Capitis Magnus
mOmHy	m. Omohyoideus
mptc	medial pterygoid crest
mPPt	m. Levator Pterygoidei
mPstP	m Pseudotemporalis Profundus
mPstS	m Pseudotemporalis Superficialis
mPt	m. Pterygoideus
mPtTy	m. Pterygoideus Typicus
mPtTyD	m. Pterygoideus Typicus Dorsal
mPtTyML	m. Pterygoideus Typicus Middle Lateral
mPtTyMM	m. Pterygoideus Typicus Middle Medial
mPtTyV	m. Pterygoideus Typicus Ventralis
mReCaPP	m. Rectus Capitis Posterior Profundis

mReCaPS	m. Rectus Capitis Posterior Superficialis
mSp	m. Spinalis
mSpCa	m. Spinalis Capitis
mSspCa	m. Semispinalis Capitis
mSteHy	m. Sternohyoideus
mSty	m Stylohyoideus
msep	median septum
msul	median sulcus
mTrap	m. Trapezius
mTrv	m. Transversalis
mVec	m. Verticalis
MX	MAXILLA
n	external nares
NA	NASAL
ns	neural spine
ntch	notch
oc.proat.lig	occipital proatlas ligament
occd	occipital condyle
odpr	odontoid process
OP	OPISTHOTIC
orb	orbit
PAL	PALATINE
pal.tr	palatal tooth row
pap	filamentous papilla
PAR	PARIETAL
par.crt	parietal crest
par.for	parietal foramen
PAT	PROATLAS
path	pathology
PMX	PREMAXILLA
pmx.t	premaxillary tooth
PO	PROTIC

pocc	paroccipital process of the opisthotic
POFR	POSTFRONTAL
PORB	POSTORBITAL
pozyg	postzygapophyses
ppj	posterior process of the jugal
pr	process
PRE	PREARTICULAR
prezyg	prezygapophyses
PRFR	PREFRONTAL
PSPH	PARASPHENOID
psro	parasphenoid rostrum (cultriform process)
PT	PTERYGOID
ptb	posterior temporal bar
ptfl	pterygoid flange
ptne	pterygoid neck
QJ	QUADRATOJUGAL
qj.for	quadratojugal foramen
QU	QUADRATE
qucd	quadrate condyle
ret	reteroarticular process
ri	ridge
RIB	RIB
sba	secondary bone apron (lingual surface)
sbb	secondary bone band
sbs	secondary bone skirt (labial surface)
se	seam
skin	skin
sl	slice
SMX	SEPTOMAXILLA
SO	SUPRAOCCIPITAL
sorb	suborbital fenestra
sosm	suborbital section of the maxilla

sot	spheno-occipital tubercle
sp2sp.n	space for the 2 nd spinal nerve
SQ	SQUAMOSAL
ssp	suprascapula cartilage
ST	STAPES
SUR	SURANGULAR
sym	symphysis
t	tooth
tenb	tendinous band
ten	tendon
tong	tongue
tpr	transverse process
tro	trough
tub	tubercle
utb	upper temporal bar
utf	upper temporal fenestra
V3	VERTEBRA 3
V4	VERTEBRA 4
V5	VERTEBRA 5
V6	VERTEBRA 6
vi	vidian groove
VO	VOMER
vo.t	vomerine tooth
vplj	ventral projection of the lower jaw
vtsep	ventral transverse septum
wf	wear facet